

Stigmella naturnella* (Klimesch, 1936) (Lepidoptera, Nepticulidae) a fast-spreading European leafminer of *Betula*, with a revised key to linear leafmines on *Betula

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Abstract. *Stigmella naturnella* (Klimesch, 1936), a leafminer of *Betula*, is here recorded as new for France, Croatia, Ukraine, Belgium, and the Netherlands. Since 2018, it has expanded its range into the last two countries, partly based on numerous online observations. Its distribution history is reviewed, the species is diagnosed and its life history is described. A lectotype is designated for *Nepticula naturnella* Klimesch, 1936. The species is widespread in the Palearctic, from Japan to the North Sea, with a maximum of 1.63% variation in its DNA barcode. Legacy leafmine records for Germany are reviewed, resulting in the confirmation of its occurrence in Baden-Württemberg already in 1935, but other old records are rejected. It is one of the few Nepticulidae species that hibernate as adult, a possible contributing factor to its expansion. As the leafmines may be confused with other *Betula* mining species, a revised key to the leafmines of European *Stigmella* species on *Betula* is provided. *Stigmella glutinosae* (Stainton, 1858) and *S. alnetella* (Stainton, 1856), usually feeding in *Alnus*, are both recorded to occur occasionally on *Betula* and are included in the key.

Introduction

As for many other organisms, spread and invasions have been recorded recently for several leafmining moth species. A number of species have invaded Europe from other continents, aided by human activity, and have often spread quickly over the continent, hostplant availability permitting. Examples are *Macrosaccus robiniella* (Clemens, 1859) and *Parectopa robiniella* Clemens, 1863 that invaded Europe probably with the aid of airplanes in the 1970s or 1980s of the last century, and which have since spread over a large part of Europe, finding their hostplant *Robinia pseudoacacia* L. widely distributed (Mally et al. 2021). Two North American leafminers of walnuts and related Juglandaceae were recently noted for the first time respectively in Italy (*Coptodisca lucifluella* (Clemens, 1860)) (Bernardo et al. 2011, 2015) and Hungary (*C. juglandiella* (Chambers, 1874)) (Takács et al. 2020), and both have since also been found in neighbouring countries, suggesting spread through dispersal (Takács et al. 2020; Tomov 2020; Haslberger and Segerer 2021; Huemer 2021; Laštůvka et al. 2021).

Further examples in leafmining Lepidoptera are seen in European species that have expanded their range due to the widespread planting of their hosts in parks and gardens beyond their native habitat: for example *Antispila treitschkiella* (Fischer von Röslerstamm, 1843) on *Cornus mas* L.

(van Nieukerken et al. 2018), *Phyllonorycter leucographella* (Zeller, 1850) on *Pyracantha* species (Šefrová 1999; Walczak et al. 2010); and several *Acer* feeding species (van Nieukerken et al. 2006b; Corver et al. 2011; Huisman and Muus 2020).

Whereas in these cases climate change may have been a major factor in the spread, other causes are more complex to explain. Spread of leafmining species on hostplants that have always been native in the region are probably better indicators of climate change, such as *Stigmella nivenburgensis* (Preissecker, 1942) on *Salix* species and several *Phyllocnistis* species feeding on *Salix* and *Populus* that have expanded recently in NW Europe (van Nieukerken et al. 2017; Prick et al. 2018; van Nieukerken and Wullaert 2018a, b; Schulz and Fähnrich 2019; Wullaert 2019). Also the oak leafmining nepticulid *Ectoedemia quinquella* (Bedell, 1848) is shifting its distribution northwards in the Netherlands (Alders and Donner 1992; van As and Scheffers 2013).

On *Betula* until now, we did not see any clear northward shifts of leafmining species, which is to be expected, as *Betula* itself is a more northerly genus (San-Miguel-Ayanz et al. 2015) with few southern herbivore specialists (Ellis 2022). An exception may be *Stigmella sakhalinella* Puplesis, 1984, of which there are indications of a northward shift as seen from relatively recent first records in northern Europe, Norway in 1988 (Aarvik et al. 1997), Sweden 1990 (Svensson 1992), Lithuania 2004 (Anisimov and Stonis 2008), Denmark 2009 (Buhl et al. 2011), Estonia 2009 (Jürvete 2011; Jürvete and Šunap 2020), Ireland 2015 (Langmaid and Young 2016) and Finland in 2016 (Aarvik et al. 2021) (details unpublished, mines collected by Mikhail Kozlov, identified by the author, see Fig. 63 and BOLD record RMNH.INS.31157).

Stigmella naturella (Klimesch, 1936) is the only *Betula* feeding species of Nepticulidae in Europe with a more southerly distribution. It was described from the southern Alps in Italy, South Tyrol from the warm valleys of the Vintschgau (Venosta) (Klimesch 1936). For many years very little information was added about this species, apart from a treatment by Klimesch (1948), who described the male genitalia, and a few odd records of leafmines (Skala 1937, 1939; Buhr 1940a, b) that were subsequently mostly neglected or believed to be incorrect. The species was rarely recorded from Central Europe and considered to be a rare and thermophilous species (Szőcs 1973; Laštůvka and Laštůvka 1991, 1997). The fact that the leafmines of *S. naturella* were considered to be almost impossible to distinguish from similar ones such as *S. confusella* (Wood & Walsingham, 1894) added to the poor state of knowledge of the species.

Meanwhile *S. naturella* was described again as *Astigmella dissona* Puplesis, 1984 from the Far East of Russia (Puplesis 1984a, b), a synonymy that was later recognised when the species appeared to be common in the Volga area in European Russia (van Nieukerken et al. 2004). Only recently a few odd records were published from Europe north of the Alps: one record in Poland and three in Germany (Baran 2013; Guggemoos et al. 2018; Sobczyk et al. 2018; Segerer et al. 2019). After learning how to recognise mines of this species from my work on the Russian leafmines, I found *S. naturella* mines in South Tyrol, and to my surprise in 2017 in western France, far from the Alps. An even bigger surprise was the discovery of photographs of leafmines resembling this species on the Netherlands' observation platform waarneming.nl. Although I was sceptical at first that they could be attributed to *S. naturella*, I set out in the autumn of 2020 to search for such *Betula* mines in the Netherlands. This led to the discovery that *S. naturella* had entered the Netherlands unobserved over the last few years and had already established populations throughout its southern half, often having become one of the commonest leafminers on birch. The Belgian observation platform waarnemingen.be also contained several misidentified mines that



Figure 1. *Stigmella naturnella*, live female, The Netherlands, Rijssen, emerged 14.x.2022 (photo Gerwin van de Maat).

could be attributed to this species and a few photos of live adults were identified as *S. naturnella*. These observations were announced on two online platforms (van Nieukerken 2020a, b). In this paper all records are reviewed, together with a history of the species spread, and a diagnosis of the species is provided. As the leafmines can easily be confused with other species, special attention is paid to the diagnostics of *Stigmella* mines on *Betula*, aided by the provision of a key.

Material and methods

Collecting

Material collected by me before 2020 was found during general leafmine searching, not focussed particularly on *Betula*. In autumn 2020 (September–October) collecting in the Netherlands was devoted to *Betula* miners specifically to study the distribution of *Stigmella naturnella*. Six full days of field work were carried out in the provinces of Utrecht, Gelderland, Noord-Brabant and Zuid-Holland; in addition some observations were made during other activities in Limburg; in 2021 and 2022 a few further records were obtained. Mature and juvenile trees and seedlings were searched for leafmines, and samples of all species of Nepticulidae were collected, whether vacated or with larvae. Leafminers of other groups than Nepticulidae were noted and only occasionally collected. In most cases photographs were taken of the various species in the field. Leaves with mines were gathered in plastic bags or small containers. Some larvae, especially those that had died or looked in poor condition, were dissected from their mines and preserved in 96% ethanol for molecular and morphological studies. Samples of leaves with leafmines were dried using a plant press and subsequently stored in glassine envelopes.

Rearing

Collected leaves with occupied leafmines were kept in small jars or polystyrene bags, with some moss, earth and/or paper tissue added, until the larvae had left their mines. After that the leaves were taken from the rearing jars and pressed and dried as vouchers. Adults were reared

from the cocoons in the same containers, occasionally adding some moisture. *Stigmella naturella* adults emerged within a few weeks, no hibernation occurred, and rearing jars were kept indoors until emergence. Rearing jars with cocoons of other species were kept in a refrigerator at ca. 4 °C between November and early March and then brought indoors until emergence. Emerged adults were mounted freshly after allowing them to harden for at least a day, or overnight.

Materials and observations

In Leiden all larval specimens, samples of leafmines and the majority of adults received a registry number in the form RMNH.INS.#####. Most field collections and observations were also registered on the observation platform waarneming.nl and received a field number (EventId) in the form EvN no 2020### (year and serial number between 001 and 999) for each combination of locality and hostplant species (or as short form EvN2020###). For multiple species on a single host, an extra number follows a dash, letters indicate destination of each sample (K=breeding, M=molecular tissue sample, H=herbarium, pressed leaves with vacated or unfinished mines). Examples are EvN no 2020062-1K, EvN no 2021152-3H.

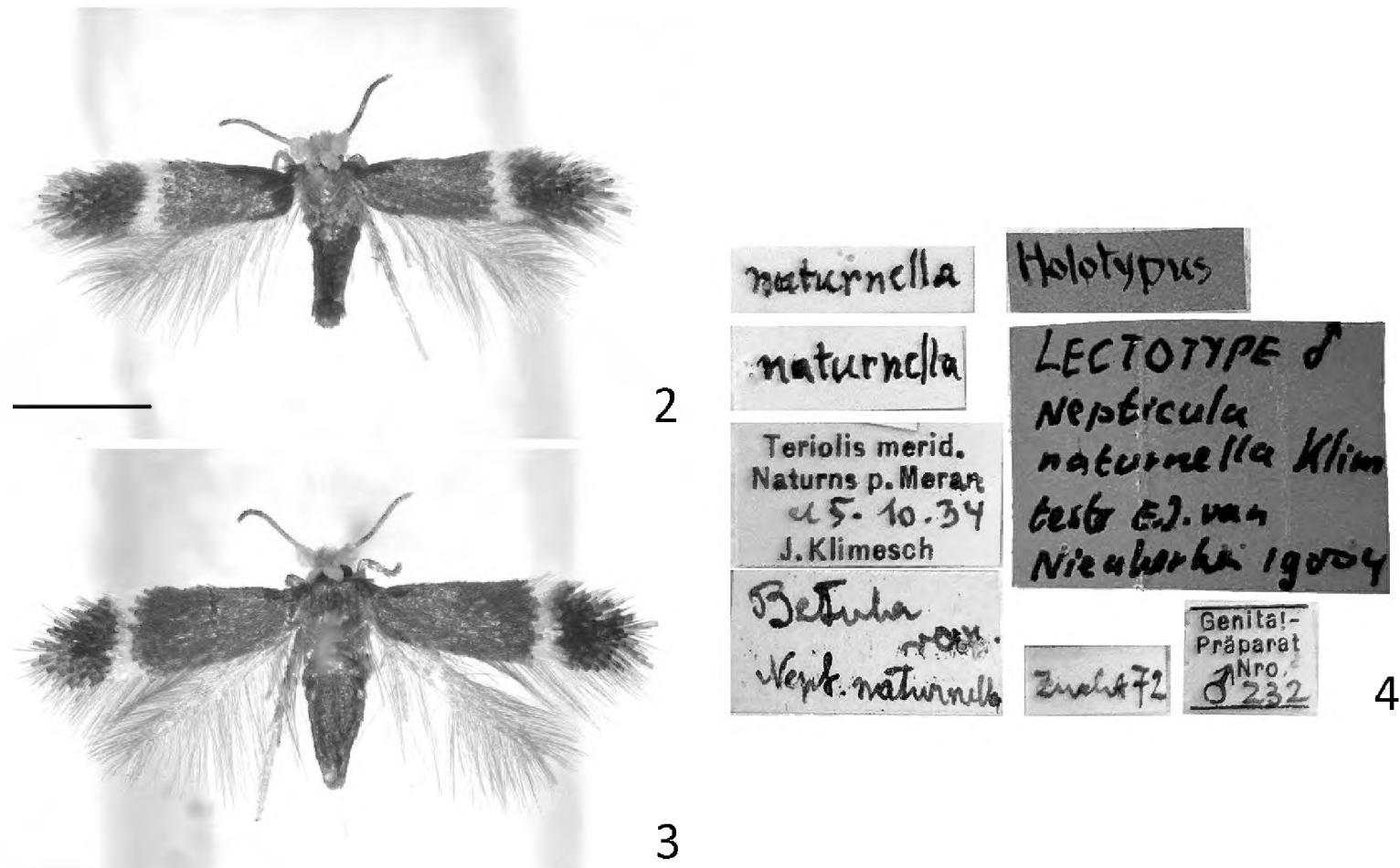
Some material, both adults and leafmines, was borrowed from other institutes or received from various colleagues in identification loans over the course of many years. Some data were obtained from databases: viz. the Netherlands Lepidoptera database “Noctua” (via Dutch Butterfly Conservation) and the database of the Tiroler Landesmuseen Ferdinandeum (via Peter Huemer). Many records were obtained from the Dutch and Belgian online observation platforms (respectively <https://waarneming.nl/>, Observation International and local partners 2022a and <https://waarnemingen.be/>, Observation International and local partners 2022b), often originally registered under different identifications. Some records were also found on the international platform <https://www.inaturalist.org/> (iNaturalist community 2022), but none on <https://observation.org/>. Many of these records could be re-identified or confirmed if suitable photographs were uploaded, and I was able to validate or correct records from <https://waarneming.nl/> and <https://www.inaturalist.org/>, Carina van Steenwinkel validated records on <https://waarnemingen.be/>. Records were used only when validated, or verified by me. Obvious duplicate records were omitted. Data were included up to November 2022.

Records of DNA barcoded specimens were downloaded from BOLD SYSTEMS (Ratnasingham and Hebert 2007) and are brought together in a publicly available dataset (<https://doi.org/10.5883/DS-STIGNATU>) and in Suppl. material 1.

A detailed dataset of material, observations and literature records was uploaded via NLBIF to GBIF (<https://doi.org/10.15468/9u5f59>). The material listed below includes only that which has been examined by me. This material is organised by country, and for those countries with much information also by province. Data of material for other species, referred to in the text and figures is listed in the appendix, and also in the GBIF dataset.

Molecular methods

DNA barcoding followed the procedures at our laboratory as described by van Nieukerken et al. (2012) and Doorenweerd et al. (2015). Genbank accession codes were added to the datasets cited above and in Suppl. material 1. A few DNA barcode sequences originated from other sources, viz. projects by Peter Huemer (TLMF), Christian Wieser (Landesmuseum Kärnten, Austria), Andreas Segerer (ZSM) and from the Centre for Biodiversity Genomics, Guelph. Specimens from the last source were collected with Malaise traps, for a description of the protocol see deWaard et al. (2019)



Figures 2–4. *Stigmella naturella* 2. male, The Netherlands, Wolfheze, RMNH.INS.17215l; 3. female, Goirle, The Netherlands, RMNH.INS.17214; 4. Lectotype labels (photo Andreas Segerer). Scale bar: 1 mm (2, 3).

The Neighbor Joining tree was prepared with tools provided by BOLDSYSTEMS (Ratnasingham and Hebert 2007) and edited with Adobe Illustrator CS5.

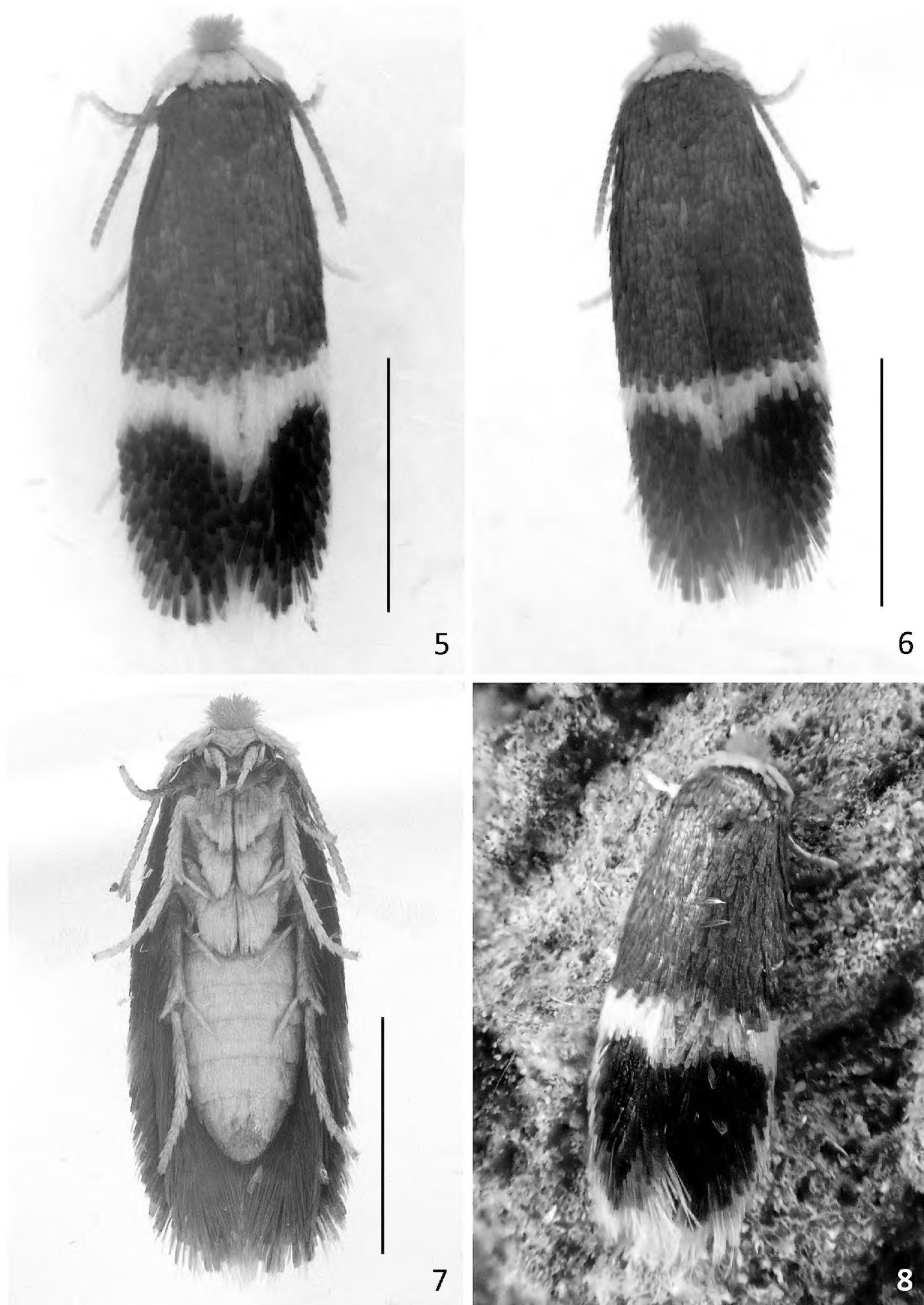
Morphology

Genitalia were prepared according to our standard procedures, usually including DNA extraction, as described earlier in detail (van Nieuwerken 1985; van Nieuwerken et al. 2010).

Measurements of moths, genitalia and leafmines were taken with measuring tools in Carl Zeiss Axio-Vision software on photographs, see below. For a sample size of 4 and higher, mean, standard deviation and sample size are provided between brackets. Details of measurements are given in Suppl. material 2.

Illustrations

Unless otherwise mentioned, all photographs were taken by the author. Photographs of moths, leafmines, genitalia slides and larval slides were taken with a Zeiss AxioCam digital camera attached, respectively, to a Zeiss Stemi SV11 stereo-microscope, a motorized Zeiss SteREO Discovery V12 or a Zeiss Axioskop H, using Carl Zeiss AxioVision software version 4.8 or 4.9. Field photographs were taken with a Canon EOS 600D prior to 2020, in 2020 with a Nikon D70 or a Mobile phone and in 2021 with a Canon EOS 850D. For photographing leafmines with the Zeiss set up, dark field illumination was used. Images were edited with Photoshop CS5, mainly to obtain a more even background, better lighting and some sharpening was added; some illustrated photographs were composed from a number of photographs by Photoshop photomerge. Plates were composed with Photoshop CS5. The distribution maps were prepared with QGIS 3.10.



Figures 5–8. *Stigmella naturella*, live adults **5.** Male, 4.x.2020, Netherlands, Wekerom, RMNH.INS.25268; **6, 7.** Female, 1.x.2020, Netherlands, Soest RMNH.INS.17204; **8.** Hibernating adult under bark of *Platanus*, Belgium, Antwerp, 6.ii.2020 (photo Stijn Baeten), <https://waarnemingen.be/observation/185190974/>. Scale bars: 1 mm.

Abbreviations

EvN	Erik J. van Nieukerken;
HNHM	Hungarian Natural History Museum (Termeszettudományi Múzeum), Budapest, Hungary;
JE	Herbarium Haussknecht, Friedrich Schiller University Jena, Germany;
NHMUK	Natural History Museum London, UK;
RMNH	Naturalis Biodiversity Center, Leiden, Netherlands;
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany;
TLMF	Tiroler Landesmuseum Ferdinandeum, Innsbruck, Austria;
ZIN	Zoological Institute, St Petersburg, Russia;
ZMUC	Zoological Museum, Natural History Museum of Denmark, Copenhagen, Denmark;
ZSM	Zoologische Staatssammlung München, Germany.

Results

Stigmella naturnella Klimesch

Local names. zuidelijke berkenmineermot (Dutch), südliche Birkenminiermotte (German), szőrösnyír-törpemoly (Hungarian).

Nepticula naturnella Klimesch, 1936: 205. Lectotype ♂ (here designated), Italy: “Teriolis merid., Naturns p. Meran, el 5.10.34, J. Klimesch / Betula verr., Nept. naturnella / Zucht 72/ Genital-Präparat Nro ♂ 232/ Holotypus”, [larvae collected September 1934] (labels Fig. 4) (ZSM) [examined].

Astigmella dissona Puplesis, 1984a: 112. Holotype ♂, Russia, Primorskiy Kray, 20 km E Ussuriysk, Gornotayezhnoe, 28.v.1983, leg. R. Puplesis, genitalia slide no. AG 403 (ZIN) (synonymised by van Nieukerken et al. 2004a: 133).

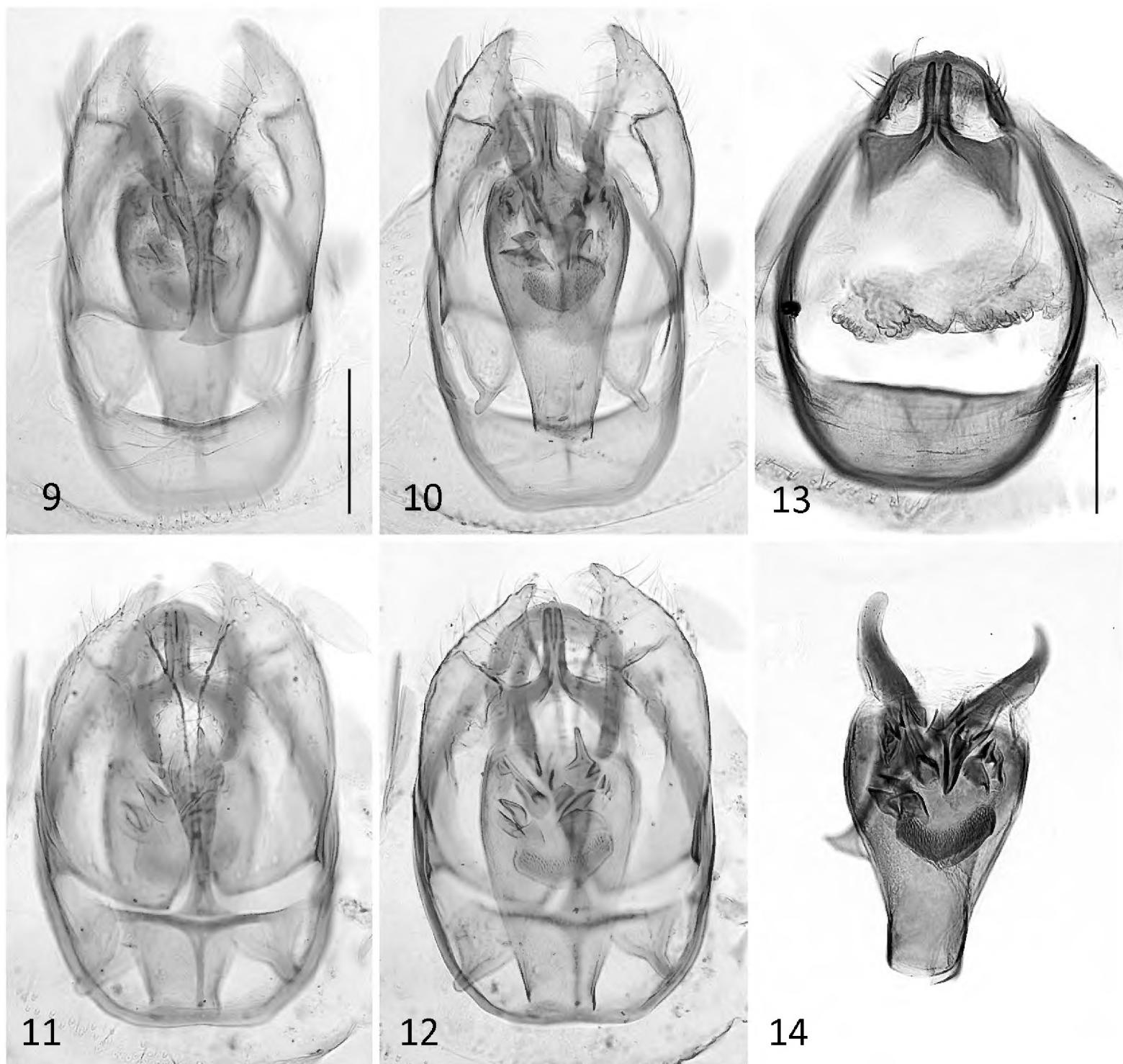
“*Nepticula argentifasciella* Klimesch”: Skala 1936: 11. Unavailable name and Junior Homonym of *Nepticula argentifasciella* Braun, 1912.

Stigmella naturnella Klimesch 1948: 65 [recombination, male genitalia], van Nieukerken et al. 2004 [Synonymy, European Russia]; Stonis and Rocienė 2013: 2, 3 [photographs male genitalia holotype *A. dissona*].

Stigmella dissona Puplesis 1994: 58 [recombination, redescription].

Diagnosis. *Stigmella naturnella* adults resemble most other *Stigmella* species with a fascia, pale head and white collar superficially, including other *Betula* miners in the *S. betulicola* group. Characteristic is the combination of a distinct fringe line, white fringe, rather shining fascia, and a relatively short antenna in both sexes, reaching only halfway to the fascia. The basal part of the forewing may vary from grey to black with a blue iridescence. Those with grey can be confused with *S. tityrella* or *S. carpinella*, but these have usually the last part before the fascia darker and the antennae distinctly longer, reaching the fascia. Species in the *Stigmella betulicola* group do not have a fringe line and the males have longer antennae. Male genitalia are very characteristic by shallow uncus, connected gnathos arms and shape and number of cornuti, female genitalia much less so, but the very long posterior apophyses are notable. For mines and larvae see below.

Description. Male (Figs 2, 5). Forewing length 1.7–2.2 mm (2.0 ± 0.2 , n=6), wingspan ca. 3.9–4.8 mm. Head. Frontal tuft pale orange, collar conspicuous, cream white. Scape large, cream white. Antenna short, reaching slightly more than halfway between wing base and fascia; with 18–21 articles (19.0 ± 1.2 , n=5). Thorax and forewings basal to fascia shining dark grey to almost black; a narrow silvery white fascia slightly beyond middle, usually constricted in middle; apical area contrasting darker black compared to wing base; a fringe line of black scales separates the silvery white terminal fringe. Hindwing grey. Abdomen black, no visible anal tufts.

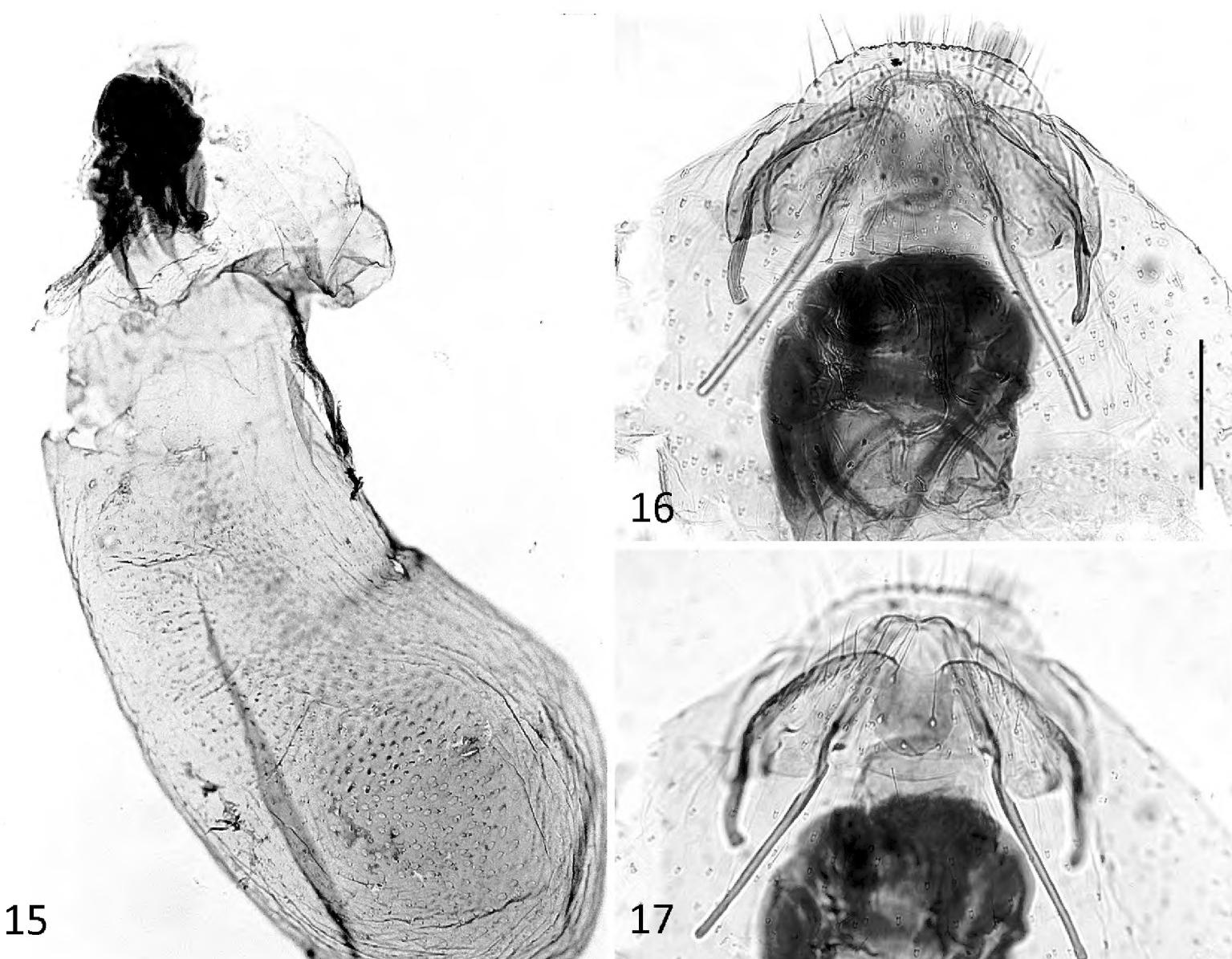


Figures 9–14. *Stigmella naturella*, male genitalia, ventral aspect. **9, 10.** Slide EvN5268; **11, 12.** Slide EvN5341; **13.** Genitalia without valvae and phallus, slide EvN3302; **14.** Phallus, slide EvN3303. Scale bars: 100 µm (9–12 top left, 13, 14 top right).

Female (Figs 1, 3, 6, 7). Forewing length 2.1–2.3 mm (2.2 ± 0.1 , n=6), wingspan ca. 4.4–5.0 mm. Antenna very short, reaching less than halfway between wing base and fascia; with 17–18 articles (17.2 ± 0.4 , n=6). Abdomen slightly tapering.

Male genitalia (Figs 9–14). Vinculum with narrow ventral plate; tegumen band-shaped; uncus slightly indented; gnathos with distal arms very close, appearing almost as single structure. Valvae broad, slightly acuminate. Juxta anteriorly arrow shaped, posteriorly ending in two arms. Phallus distally widened, with ca. 8–10 strong cornuti.

Female genitalia (Figs 15–17). Ovipositor blunt. No visible anal papillae. Tergum 8 with indented posterior margin, with central sclerotised plate, few setae along margin. Narrow posterior

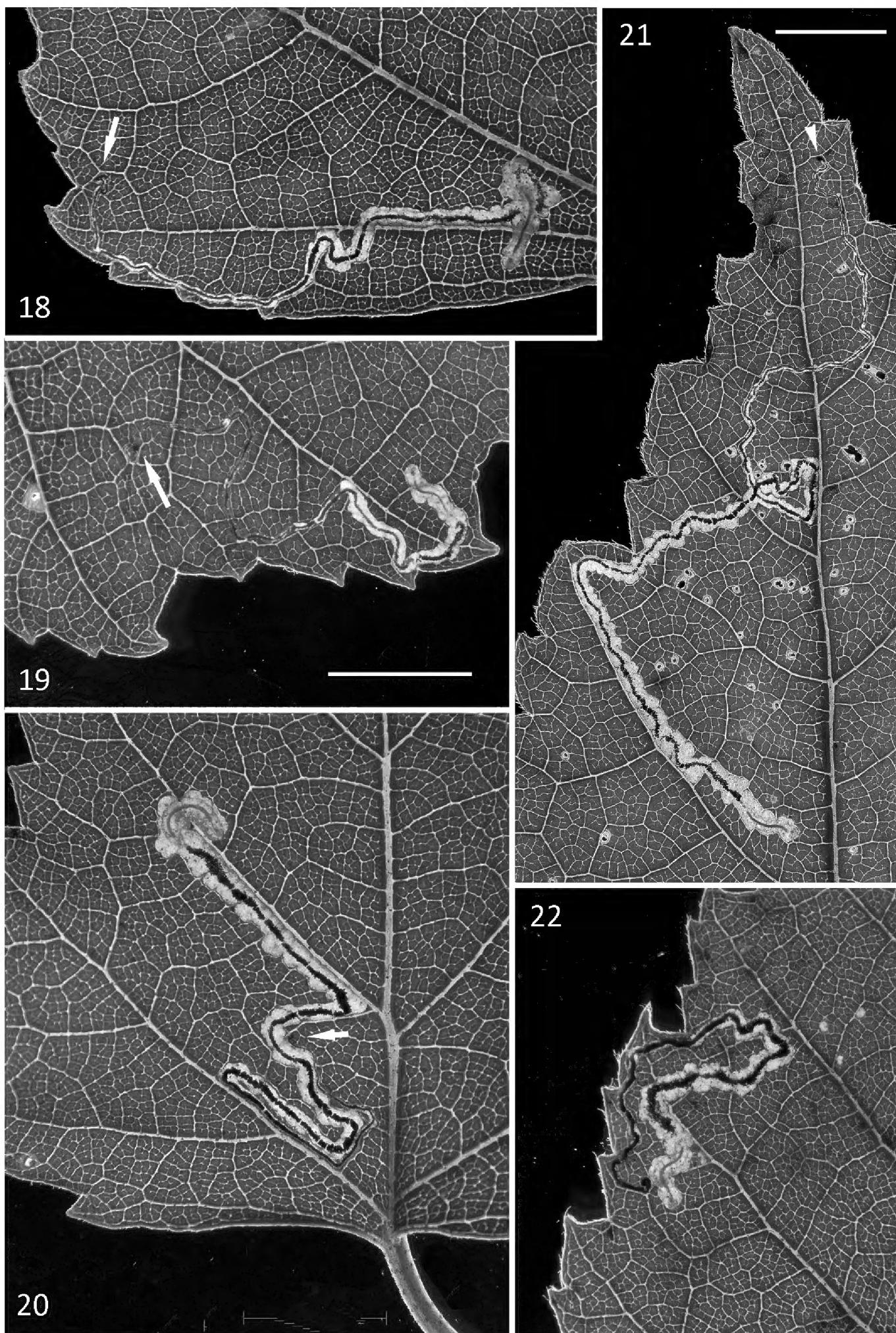


Figures 15–17. *Stigmella naturnella*, female genitalia, ventral aspect **15**. Bursa copulatrix, slide VU1874; **16, 17**. Abdominal tip, respectively more ventrally and more dorsally in focus, slide EvN5342. Scale bar: 200 µm (**16, 17**).

apophyses reaching distinctly beyond anterior apophyses in abdomen. Vestibulum folded, staining strongly with chlorazol. Ductus spermathecae not coiled. Bursa copulatrix rather long, covered with small spines and pectinations.

Biology. Host plants. In Europe *Betula pendula* subsp. *pendula* Roth and *B. pubescens* Ehrh. and their hybrids, from East Asia reported from *B. pendula* subsp. *mandshurica* (Regel) Asburner & McAll. (*B. platyphylla* Sukaczev) and *B. dahurica* Pall. (adults found on trunks, Puplesis 1984a, b). In the botanical garden of Linz, leafmines were also observed on the eastern Palearctic taxa *B. pendula* subsp. *mandshurica* and *B. utilis* D. Don subsp. *jacquemontii* (Spach) Ashburner & McAll. (see Klimesch (1990) and material examined). Much more frequently observed on *B. pendula* than on *B. pubescens*, also most literature references cite *B. pendula* (often under the old name *B. verrucosa*), but although Baran (2013) suggested that his record from *B. pubescens* was a new host record, it had been recorded from *B. pubescens* before (Skala 1939; Wörz 1958), records that are here partly confirmed.

Egg deposited on leaf upper- or underside, 67% were found on the underside (n=315), but the percentages differ per population, although almost always both positions occur when ten or more



Figures 18–22. *Stigmella naturella*, occupied leafmines, seen from above, with dark field illumination; all from The Netherlands **18, 19, 22.** Wekerom, De Valouwe, 16 Sep. 2020, *Betula pendula*, EvN no 2020062-1; **20.** Goirle, Gorp en Roovert, 30 Sep. 2020, *B. pendula*, EvN no 2020083-1; **21.** Soest, Korte Duinen, 23 Aug. 2021, *B. pubescens*, EvN no 2021121. Scale bars: 5 mm (all but 21 on same scale), arrows point at egg position (upper- or underside of leaf).

mines per population are examined. The egg may be deposited at any place of the leaf, but most frequently away from the midrib or large veins; the egg capsule is conspicuous and dark brown after the larva has hatched (Figs 25, 26).

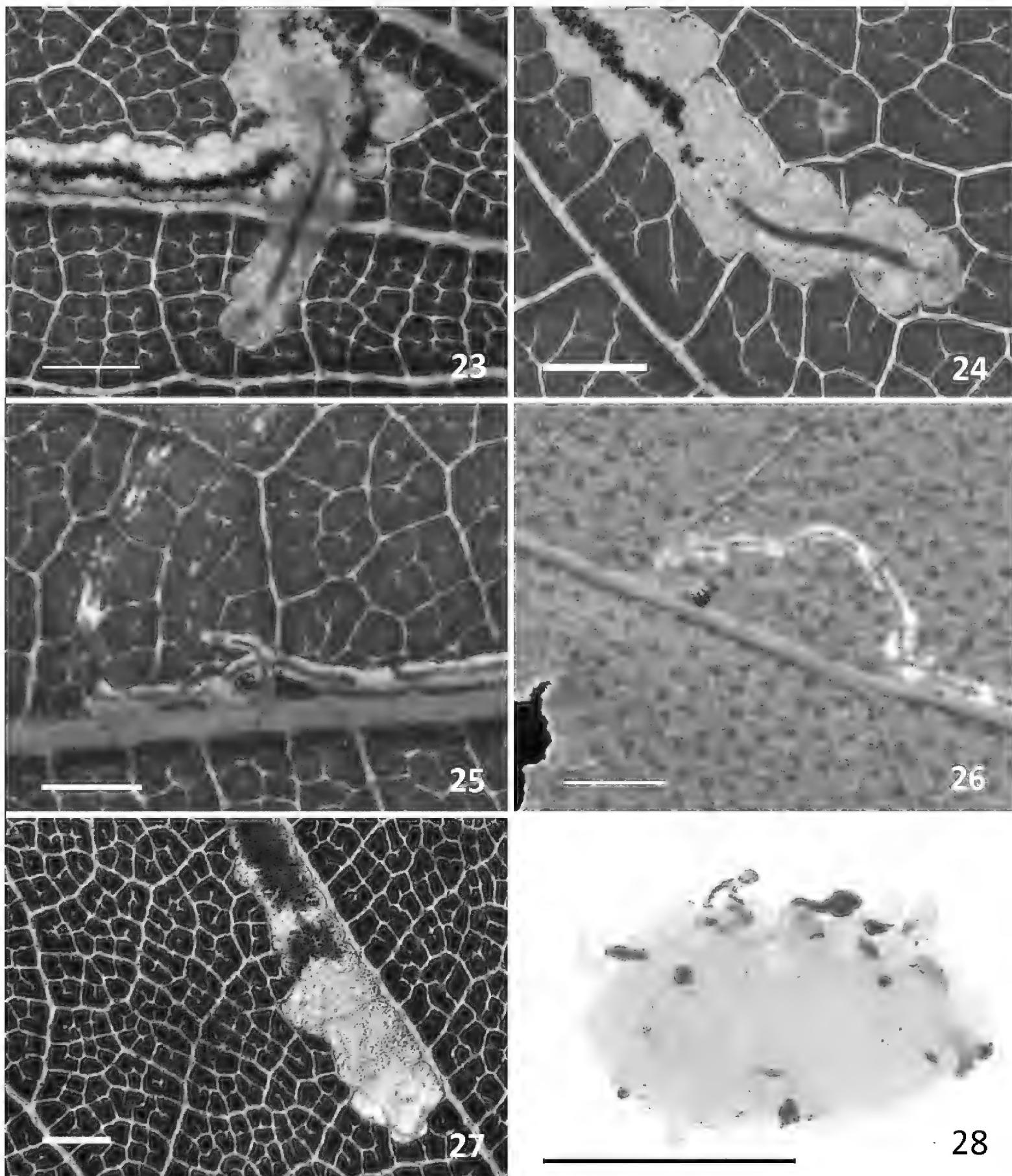
Leafmine (Figs 18–27, 29–34). A linear or gallery mine with variable length and frass disposition. From the egg the mine often runs straight away, or makes a single loose bend around the egg. The mine often does not follow parts of veins or the leaf margin, but some mines do follow veins for a shorter or longer stretch. The early mine starts in the spongy parenchyma layer, often resulting in the initial part of the mine appearing green from above, outside the frass line. This arrangement is particularly frequent on *Betula pubescens*, but many mines do not exhibit the green appearance. Frass varying from a narrow central line to a wider band of dispersed frass; in the early part of the mine it occasionally fills its entire width. The mine may be rather contorted, only occasionally crossing itself, and rarely crossing the midrib. The exit slit is invariably on the upper side of the leaf in nature. The very few mines (2–3) where an underside slit was observed, where mines that were completed by the larva in captivity after collecting; in these cases the leaf probably did not stay in its natural position, light conditions were poor, which may explain why the larva left the mine at the leaf underside. The final larval chamber often is buckled. Mines with an upperside egg and a green part at the start are the easiest to determine as *S. naturnella*, see below. Total length of mine 22.0–52.9 mm (34.0 ± 7.8 , n=27), width of final larval chamber 0.9–1.4 mm (1.0 ± 0.1 , n=27).

Larva (Figs 23, 24). The larva feeds venter upwards. Colour white to faintly pale yellow, head capsule brown; ventral nerve chord and ganglia invisible, apart from the conspicuous brown circular suboesophageal ganglion, which is a decisive diagnostic character; in actively feeding larvae the green intestine is also conspicuous.

Cocoon (Fig. 28). White and rather flimsy.

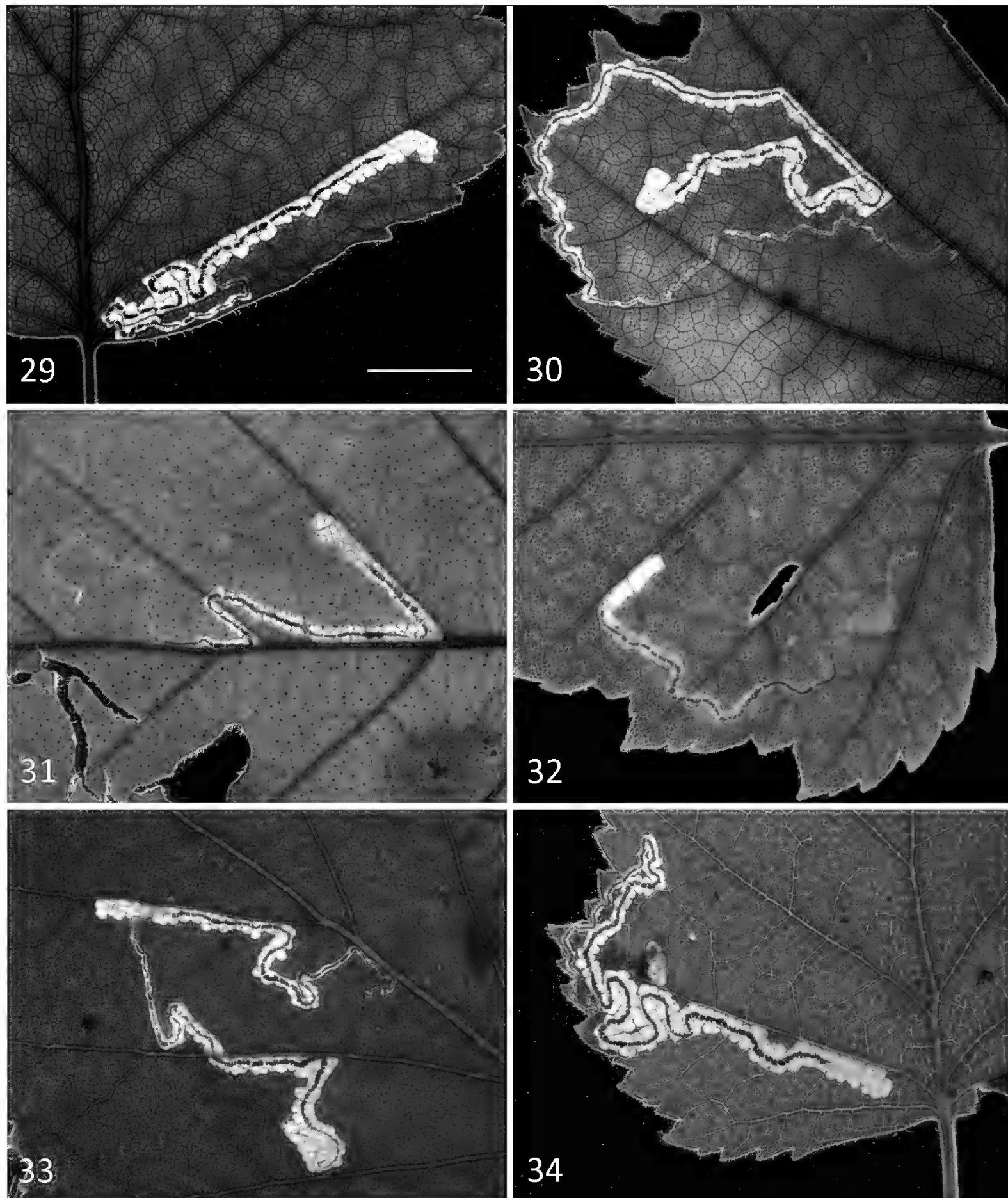
Life history. Larvae have been recorded from late-May to mid-July, and again from mid-August until October, with a single record from November. It is one of the earliest Nepticulidae larvae occurring on *Betula*, only *S. lapponica* can also be found in May and early June. Larvae seem to be most abundant in August, in the autumn only single larvae are found amongst large numbers of vacated mines. Adults have been collected or observed, after hibernation, from early April to early May, and again from 25 June almost continuously to 10 October, with a single record on 3 November. Hibernating adults have been found under the bark of trees, often *Platanus* (Fig. 8), but also on oaks, in November, January, February and March in Belgium and the Netherlands (Table 1) and in Russia (Ul'yanovsk) under bark of *Betula* on 19 April (van Nieuwerken et al. 2004). Adults reared from larvae usually emerge within 2–3 weeks after collecting; in our material from the Netherlands from 17–23 days after collecting the larva (19.09 ± 2.07 , n=11). Klimesch (1936, 1948) reported a pupal stage between 10–12 days, Laštůvka and Laštůvka (1991) reported 13 days between collecting and emergence; but only Sobczyk et al. (2018) reported a longer period of 32 days. Note that many of these data are from indoor rearing in the autumn, when temperatures outside, especially at night were gradually becoming lower than those inside. From these data it appears that *S. naturnella* has at least two generations, maybe more in some cases, but from a large part of the distribution area hardly any data are available.

Habitat and ecology (Figs 35, 36). Most localities visited by me were on sandy soil, relatively dry forests or forest margins, either dry forest with *Pinus sylvestris*, or other planted *Pinus* species, or with *Quercus robur* and *Betula* often in the undergrowth. Mines were found sometimes in *Calluna* heathland that was becoming overgrown with juvenile *Betula* trees. *Betula pendula* was usually the most



Figures 23–28. *Stigmella naturella*, biological details, all on *Betula pendula* **23.** Larva, detail of Fig. 18; **24.** Larva, detail of Fig. 21; **25.** Early part of leafmine, with upperside egg, Wekerom, data as Fig. 18; **26.** Early part of leafmine from underside, with underside egg; Italy, Naturno, 1935, coll. Wörz; **27.** Final part of mine with exit slit on leaf upperside; Soest, Korte Duinen, 23 Aug. 2021, EvN no 2021120; **28.** Cocoon, Wekerom, data as Fig. 18. Scale bars: 1 mm.

abundant birch, but *B. pubescens* was also present. In the Netherlands I often heard the cricket *Nemobius sylvestris* (Bosc, 1792) singing in these localities; this species has a comparable habitat preference. Table 2 shows the accompanying leafminer species in 36 localities with sufficient data, most



Figures 29–34. *Stigmella naturnella*, vacated leafmines, dried samples **29**. Italy, Naturno, Jun. 1935, *Betula pendula*, coll. Wörz; **30**. Italy, Naturno, Sep. 1934, *B. pendula*, coll. Wörz; **31**. Germany, Stuttgart, Willdpark, Sep. 1935, *B. pubescens*, coll. Wörz; **32**. Germany, Badenweiler, Sep. 2001, *B. pendula*, ZMA.INS. MIG.07497; **33**. Russia, Voronezh, Aug. 2017, unfinished mines, one larva barcoded, *B. pubescens*, RMNH. INS.46142; **34**. Netherlands, Wekerom, De Valouwe, Sep. 2020, *Betula pendula*, EvN no 2020062-1. Scale bar: 5 mm (all on same scale).



Figures 35, 36. Habitat of *Stigmella naturnella* 35 (top). The Netherlands, Goirle, Gorp en Roovert – Noord, 30 Sep. 2020, EventId: EvN no 2020083, many mines of *S. naturnella* on *Betula pendula* shrub; 36 (bottom). Germany (NRW), Hövelhof, NSG Moosheide, 19 Aug. 2021, in 2021 only one mine on *B. pendula* (photo Dieter Robrecht).

common were *Stigmella sakhalinella*, *S. continuella* and *S. betulicola*. In more southern localities in France, Italy and Russia, *S. naturnella* was the dominant species with no accompanying nepticulids, or just one (*S. sakhalinella* or *S. glutinosae*). Species such as *Lyonetia clerkella* (Linnaeus, 1758) or

Table 1. Observations of hibernating adults of *Stigmella naturnella* in the period 2017–2022 in Belgium and the Netherlands.

Date	Locality	#	site	observer	Link
02-Jan	BE: Antwerpen	1	<i>Platanus</i> bark	G. Logghe	https://waarnemingen.be/observation/231441880/
12-Jan	BE: Antwerpen	1♂	<i>Platanus</i> bark	R. Hendrickx	https://waarnemingen.be/observation/232262916/
23-Jan	BE: Brugge	1♂	<i>Platanus</i> bark	S. Stevens	https://waarnemingen.be/observation/232781643/
05-Feb	BE: Antwerpen	6	<i>Platanus</i> bark	S. Baeten	https://waarnemingen.be/observation/185190974/
12-Feb	NL: Bergen op Zoom	1	<i>Platanus</i> bark	V. Vandenbulcke & G. Groeneweg	https://waarneming.nl/observation/167485152/
09-Mar	NL: Putte	2	<i>Quercus</i> trunk	G. Dekkers	https://waarneming.nl/observation/135289746/
29-Nov	BE: Booischot	1	<i>Platanus</i> bark	W. Veraghtert	https://waarnemingen.be/observation/260148887/

Table 2. Species of Nepticulidae and Bucculatricidae found together with *Stigmella naturnella*, in 36 samples of *Betula* in the Netherlands (25), France (4), Italy (2) and Russia (5). The numbers are the samples where the species was present. For details see Suppl. material 3.

Species	# samples
<i>Stigmella sakhalinella</i> Puplesis, 1984	27
<i>Stigmella continuaella</i> (Stainton, 1856)	18
<i>Stigmella betulicola</i> (Stainton, 1856)	13
<i>Stigmella luteella</i> (Stainton, 1857)	10
<i>Bucculatrix demaryella</i> (Duponchel, 1840)	8
<i>Stigmella glutinosae</i> (Stainton, 1858)	3
<i>Ectoedemia occultella</i> (Linnaeus, 1767)	3
<i>Stigmella lapponica</i> (Wocke, 1862)	2
<i>Stigmella confusella</i> (Wood & Walsingham, 1894)	1
<i>Ectoedemia minimella</i> (Zetterstedt, 1839)	1

Agromyza alnibetulae Hendel, 1931 and some sawflies were often seen, but not consistently noted by me. Nepticulidae that prefer moister habitats and have a more northern distribution, e.g. *Ectoedemia minimella*, *S. lapponica* or *S. confusella* were rarely found together with *S. naturnella*, except on 10.x.1983 when J.J. Boomsma found *S. naturnella* in the Naturno area (Italy, Bolzano) together with an outbreak of hundreds of vacated mines of *S. lapponica*.

Distribution (Figs 37, 38). Central and West Europe: Austria (throughout), Belgium (new record: north-western part), Croatia (new record: Brodsko-Posavska), Czechia (Bohemia and Moravia), France (new record: Sarthe, Savoie), Germany (Baden-Württemberg, Bayern, Brandenburg, Nordrhein-Westfalen [new record], Saarland [new record], Sachsen), Hungary, Italy (Bolzano, Torino [new record], Trento), the Netherlands (new record: southern two thirds), Poland, Slovakia, Switzerland (Graubunden, Valais), Ukraine (new record: Chernihiv Oblast), Russia, from European part to Primorye (van Niekerken and Sinev 2019, 2022) and Japan, Honshu (Hirano 2013). For further details, references and history see below.

DNA barcodes (Fig. 39). DNA barcode data are available for a total of 35 specimens across the distribution area between the Netherlands and Japan. All fall within Barcode Identification Number BOLD:AAV8372, with an average distance of 0.72% and a maximum distance of 1.63%. The nearest neighbour, with 5.9% distance, is the North American *Stigmella nigriverticella* (Chambers, 1875), in the *Stigmella saginella* group. However, barcodes of the closely related

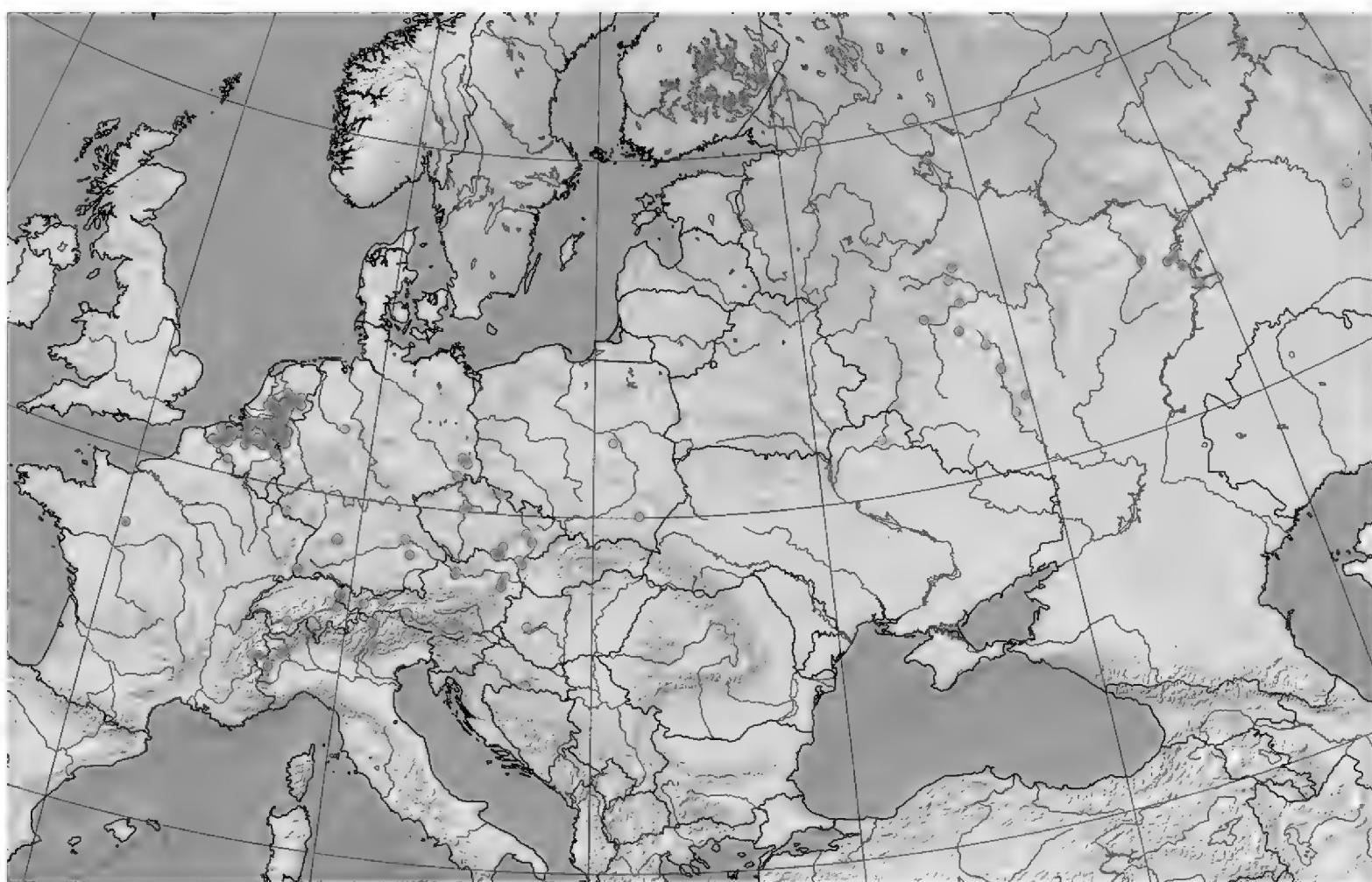


Figure 37. Distribution records of *Stigmella naturnella* in Europe and western Siberia.

Eastern Palaearctic species *S. mirabella* Puplesis, 1984 are still unknown. There is some geographical pattern visible in the NJ tree (Fig. 39, see also the haplotype network given on the BIN page, http://www.boldsystems.org/index.php/Public_BarcodeCluster?clusteruri=BOLD:AAV8372). All Dutch, French and western German DNA barcodes belong to the same cluster, together with some Austrian records, whereas the remaining Austrian records and one from Germany, Sachsen, group with an Italian and several Russian records. DNA barcodes, especially those from easternmost Russia, Primorsky Kray, show most variation, but it should be noted that these DNA barcodes were on average a bit shorter than the others (total length 510–618 base pairs). However for the region covered by the missing base pairs, the other sequences show only variability in three sites.

Nomenclature and lectotype designation. Klimesch originally intended to name the species “*Nepticula argentifasciella*”, as can be seen on some of his original mines in the collection Wörz, examined by me. However, he had crossed out that name on the herbarium sheets and replaced it by “*naturnella*”, presumably having realised that *N. argentifasciella* was a homonym of the North American *Nepticula argentifasciella* Braun, 1912 (now *Stigmella argentifasciella*). The name, however, entered the literature as a *nomen nudum*, as it was cited by Skala (1937).

Nepticula naturnella was described from an unspecified number of specimens, without selecting a holotype. I designate as lectotype the male that bears Klimesch’s dissection number 232 (labels see Fig. 4).

Remarks. *Stigmella naturnella* was placed in the *Stigmella lapponica* group by van Nieukerken (1986a) on the basis of the gnathos shape, which was later shown to be a homoplasious character (Doorenweerd et al. 2016). Puplesis (1984a, b) based his genus *Astigmella* Puplesis, 1984 on

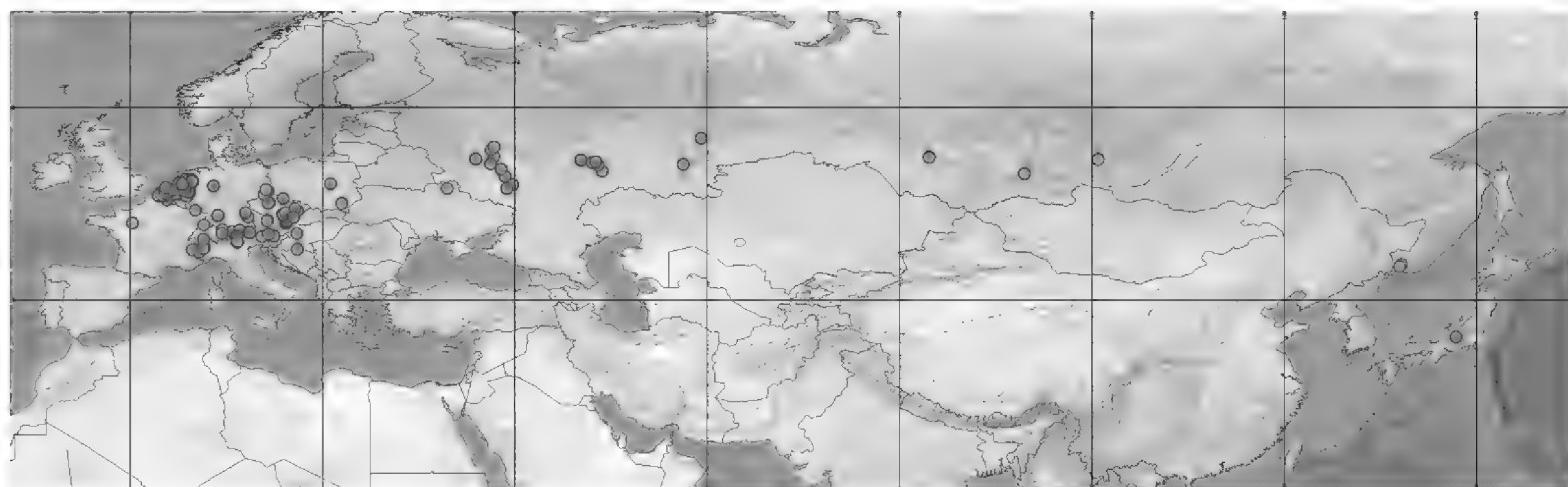


Figure 38. Global distribution records of *Stigmella naturnella*, from France to Japan (Honshu). Grid interval 20 degrees.

the synonym *A. dissona*. He separated that genus from *Stigmella* by the shorter Cu vein in the forewing and the characteristic genitalia. *Astigmella* was later synonymised with *Stigmella* (van Nieukerken 1986a). Currently *S. naturnella* is considered to form a separate species group with the East Palearctic *S. mirabella* (Puplesis, 1984), falling within the large “Non-Core” *Stigmella* clade, partly on the basis of unpublished molecular data. The *naturnella* group is close to some Asiatic *Ficus* mining species, and relatively close to the *S. ulmivora* and *S. saginella* groups.

Material examined. 23 ♂ 11 ♀ 1 sex unknown, cocoons. *B.* = *Betula*. All in RMNH, unless otherwise mentioned.

AUSTRIA • 1 ♂; Nordtirol, Fliess; 25 Jun. 2008; 47.117°N, 10.632°E; alt. 1000 m; P. Skou & D. Nilsson leg.; Genitalia slide: JCK8488; ZMUC.

GERMANY • 1 ♂; Saarland, Fraulautern, TrÜbpl.; 49.325°N, 6.7854°E; 04 Sep. 2020; A. Werno leg.; Genitalia slide: EvN5341; RMNH.INS.25341; Werno, A. , personal collection. • 1 ♀; Sachsen, Königswartha, Deichgebiet; 51.3193°N, 14.3527°E; 01 Jul. 2020; A. Werno leg.; Genitalia slide: EvN5342; RMNH.INS.25342; Werno, A. , personal collection.

HUNGARY • 1 ♀; Veszprem, Uzsa, Nyires; 46.897°N, 17.333°E; 27 Aug. 1968; J. Szöcs leg.; *B. pubescens*; emerged 13 Sep. 1968; Genitalia slide: VU1874; HNHM.

JAPAN • 1 ♀; Honshu, Nagano ken, Yamagata-mura, Karasawa; 36.158°N, 137.846°E; 13 Jun. 2009; Nagao Hirano leg.; *B. pendula* subsp. *mandshurica*; emerged 25 Jun. 2009; EventId: Host-2733; Genitalia slide: EvN4747; RMNH.INS.24747.

NETHERLANDS – Gelderland • 1 ♂ 2 ♀, 2 cocoons (plus exuviae); Wekerom, De Valouwe, Immenkampweg; 52.08977°N, 5.71459°E; 16 Sep. 2020; EvN leg.; *B. pendula*; emerged 04 Oct. 2020; EventId: EvN no 2020062-1K; Genitalia slide: EvN5268; RMNH.INS.25268, RMNH.INS.17206–17208. • 2 ♂ 1 ♀, 4 cocoons (plus exuviae); Wekerom, Wekeromse Zand, near Hoge Valksedijk; 52.09188°N, 5.67616°E; 16 Sep. 2020; EvN leg.; *B. pendula*; emerged 03–04 Oct. 2020; EventId: EvN no 2020063-1K; RMNH.INS.17209–17212. • 1 ♂; Wolfheze, Wolfhezerbos, Oude Kloosterweg; 51.997°N, 5.79882°E; 07 Oct. 2020; EvN leg.; *B. pendula*; emerged 25 Oct. 2020; EventId: EvN no 2020100-1K; RMNH.INS.17215. – **Limburg** • 1 ♀; Leudal, Sint Elisabeth, Roggelse Beek valley; 51.25462°N, 5.93057°E; 21 Sep. 2020; EvN leg.; *B. pendula*; emerged 08 Oct. 2020; EventId: EvN no 2020071-1K; RMNH.INS.17213. – **Noord-Brabant** • 1 ♀; Goirle, Gorp en Roovert - Noord; 51.50795°N, 5.07473°E; 30 Sep. 2020; EvN leg.; *B. pendula*; emerged 20 Oct. 2020; EventId: EvN no 2020082-1K; RMNH.INS.17214. – **Utrecht** • 1 ♀; Soest, Hees, Wieksloterweg, Heitje; 52.15885°N, 5.27867°E; 23 Aug. 2021; EvN leg.; *B. pubescens*; emerged 13 Sep. 2021; EventId: EvN no 2021123-K; RMNH.INS.17451. • 1 ♀, 2 cocoons (plus exuviae); Soest, Korte Duinen S. edge; 52.15107°N, 5.32399°E; 10 Sep. 2020; EvN leg.; *B. pendula*; emerged 01 Oct. 2020; EventId: EvN no 2020056-1K; RMNH.INS.17204–17205. • 1 ♀;

Soest, Korte Duinen S. edge; 52.15112°N, 5.32402°E; 23 Aug. 2021; EvN leg.; *B. pubescens*; emerged 11 Sep. 2021; EventId: EvN no 2021121-1K; RMNH.INS.17448. • 1 ♀; same locality data; *B. pendula*; emerged 11 Sep. 2021; EventId: EvN no 2021122-1K; RMNH.INS.17449.

RUSSIA – Primorsky Krai • 1 ♂; 20 km E Ussurijsk, GTS [Gornotayezhnoye, Mountain taiga station]; 43.692°N, 132.164°E; 02 Aug. 1982; R. Puplesis leg.; Genitalia slide: JCK8123. – **Samara Oblast** • 1 ♂; Zhiguli, Bakhilova Polyana, S.; 53.4°N, 49.07°E; 04 May. 1992; S.A. Sachkov leg.; Genitalia slide: EvN3303; Zolotuhin, V., personal collection. – **Ulyanovsk Oblast** • 6 ♂; Ul'yanovsk N., Pobeda forest Park; 54.37°N, 48.42°E; 19 Apr. 1995; V. Isajevy leg.; under trunks of *B. pendula*; Genitalia slide: EvN3302; RMNH.INS.23302. • 7 ♂; same data; Zolotuhin, V., personal collection.

SWITZERLAND • 1 ♂; Graubunden, GR, Trimmis, Hag; 46.9124°N, 9.560464°E; alt. 560 m; 13 Jul. 2005; A. Kopp leg.; Genitalia slide: AK5.095; Kopp, A., personal collection.

UKRAINE • 1 ♂; Chernihiv Oblast, Korop; 51.58°N, 32.98°E; 24–31 Jul. 2009; K.E. Lundsten & Bo Wikström leg.; Genitalia slide: EvN5196; RMNH.INS.25196.

Larvae and leafmines (in collection). *B.* = *Betula*. All in RMNH, unless otherwise mentioned.

AUSTRIA • 3 mines; Oberösterreich, Linz-Bauernberg, Botanischer Garten; 48.297°N, 14.277°E; 13.vi.1976; J. Klimesch leg.; *Betula jacquemontii* [= *B. utilis* subsp. *jacquemontii*]; RMNH.INS.47930.

CROATIA • 10 mines; Brodsko-Posavska, Nova Gradiška, in town; 45.254°N, 17.387°E; 17 Oct. 1983; van Nieukerken & Boomsma leg.; *B. pendula*; EventId: VU no 83505-H; ZMA.INS.MIG.11575.

CZECHIA • 2 mines; Bohemia centr., Prague; 50.12208°N, 14.49573°E; 16 Sep. 2010; V. Lanta leg.; *B. pendula*; RMNH.INS.45394. • 3 mines (photo examined); Moravia, Kotojedy, Obora; 49.264°N, 17.402°E; 30 Aug. 1961; H. Zavřel leg.; *B. pendula*; BMNH(E)425547; NHMUK.

FRANCE – Sarthe • 1 larva (slide, DNA barcoded), 7 mines; Le Mans, Arche de la Nature, Bois de Changé; 47.9885°N, 0.2604°E; alt. 85 m; 07 Oct. 2017; EvN & S. Richter leg.; *B. pendula*; EventId: EvN no 2017146-2M/H; RMNH.INS.31042(P), RMNH.INS.44072, RMNH.INS.44073. • 1 larva (ethanol, tissue collection), 5 mines; same locality data; *B. pubescens*; EventId: EvN no 2017147-1H/M; RMNH.INS.31044, RMNH.INS.44075, RMNH.INS.44077. • 11 mines; Le Mans, Arche de la Nature, Bois de Changé; 47.9888°N, 0.25835°E; alt. 83 m; 07 Oct. 2017; EvN & S. Richter leg.; *B. pendula*; EventId: EvN no 2017150-3H; RMNH.INS.44085. – **Savoie** • 4 mines; Avrieux, along D215; 45.22262°N, 6.72683°E; alt. 1375 m; 24 Sep. 2018; EvN leg.; *B. pendula*; EventId: EvN no 2018158-4H; RMNH.INS.46341. • 11 mines; Saint-Martin-d'Arc, Les Fontaines; 45.20722°N, 6.46972°E; alt. 900 m; 21–24 Aug. 2017; M. Kozlov & V. Zverev leg.; *B. pendula*; ecological sample 50; RMNH.INS.46127.

GERMANY – Baden-Württemberg • 4 mines; Badenweiler, Sophienruhe; 47.7977°N, 7.6749°E, 28 Sep. 2001; AC & WN Ellis leg.; *B. pendula*; ZMA.INS.MIG.07497. • 4 mines; Stuttgart, Willdpark; 48.77°N, 9.1°E; 01 Sep. 1935; Wörz leg.; *B. pubescens*; SMNS. • 2 mines; Zuffenhausen, Lemberg; 48.82°N, 9.14°E; [no date]; Wörz leg.; *B. pendula*; SMNS. – **Nordrhein-Westfalen** • 4 mines; Wegberg, Forst Meinweg; 51.15875°N, 6.19451°E; 23 Sep. 2021; EvN leg.; *B. pubescens*; EventId: EvN no 2021152-3H; RMNH.INS.48753. – **Sachsen** • 1 mine; Pirna, Copitz, Camping; 50.98168°N, 13.92177°E; alt. 120 m; 28 Jul. 2014; EvN leg.; *B. pendula*; EventId: EvN no 2014067-3H; RMNH.INS.47934.

ITALY – Bolzano • 4 mines (on 2 sheets); Südtirol, Naturno bei Meran, 46.656°N, 11.00200°E; “Ende 09.34, imagines e.l. A.10.34, Ende 06.35, imagines e.l. A.7.34 [*recte* 35]”; J. Klimesch leg.; *B. pendula* [*Betula verrucosa*]; SMNS (coll. Wörz). • 22 mines; Naturno, 3 km SE, N. slope; 46.62964°N, 11.02486°E; alt. 1000 m; 10 Oct. 1983; J.J. Boomsma leg.; *B. pendula*; EventId: VU no. 83437; RMNH.INS.46938. • 2 mines; Naturno, N. slope; 46.62987°N, 11.01181°E; alt. 800 m; 10 Oct. 1983; J.J. Boomsma leg.; *B. pendula*; EventId: VU no. 83433; RMNH.INS.46937. • 3 larvae, mines; Naturno, near Canal; 46.63°N, 11.025°E; 24 Jun. 1985; J.J. Boomsma leg.; *B.*; RMNH.INS.12248. • 10 mines; Völlan, 2 km S Lana; 46.59373°N, 11.15197°E; alt. 670 m; 10 Jul. 2005; EvN leg.; *B. pendula*; EventId: EvN no 2005064-H; RMNH.INS.41069. – **Torino** • 4 larvae (ethanol, tissue collection, DNA barcoded), 55 mines; Issiglio, along SP61; 45.44865°N, 7.73024°E; alt. 750 m; 02 Oct. 2018; EvN leg.; *B. pendula*; EventId: EvN no 2018242-1M/H; slide: RMNH.INS.31263–31266, RMNH.

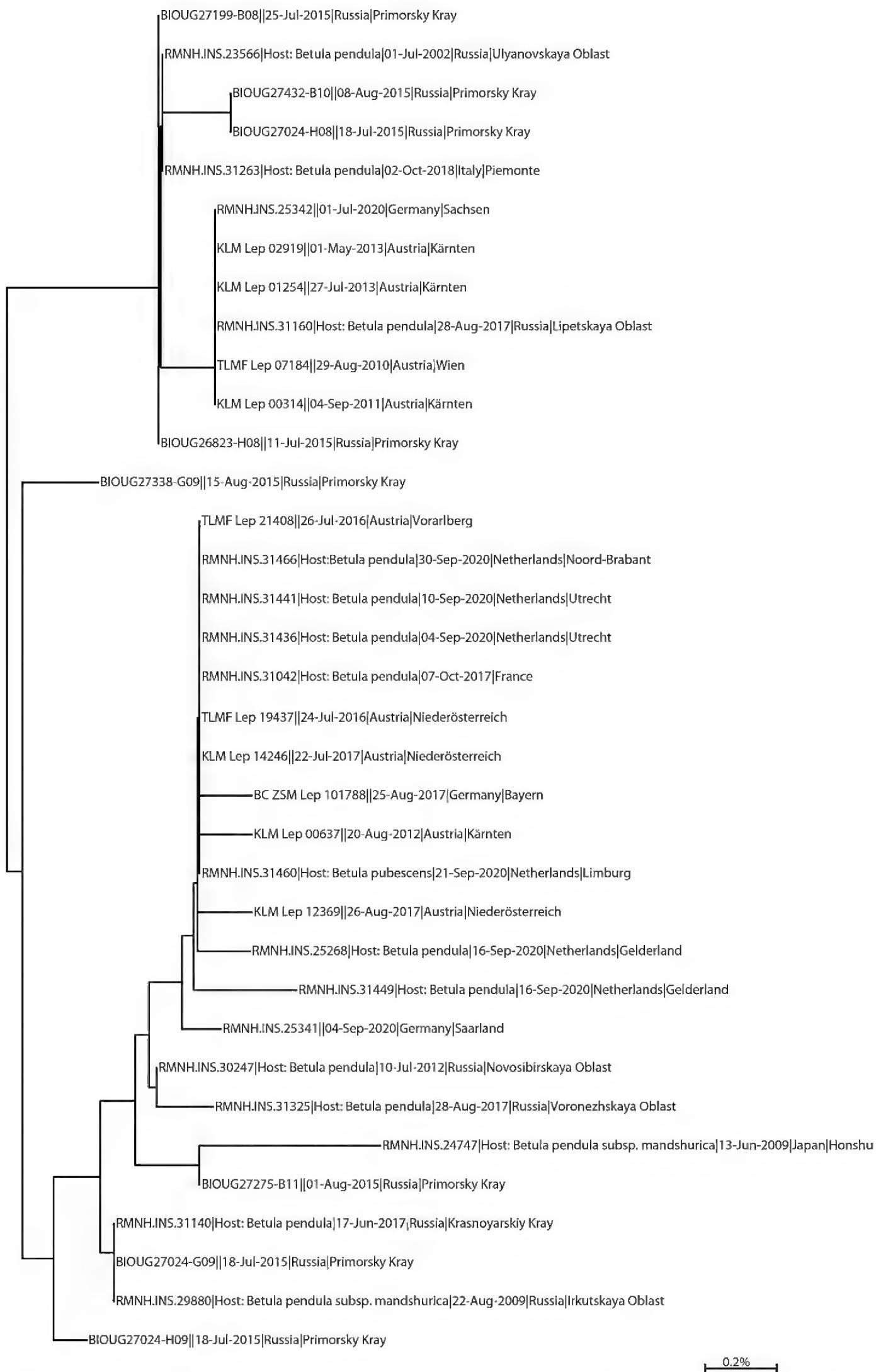


Figure 39. Neighbor Joining tree of partial COI sequences (DNA barcodes) of *Stigmella naturnella*, under the KP2 model. The labels provide data on Sample Id, Host (if known), Collection date, Country, Province.

INS.46501–46502. • 10 mines; Valle del Chisone, Perosa Argentina, rivervalley N of city; 44.96208°N, 7.18461°E; alt. 627 m; 30 Sep. 2018; EvN leg.; *B. pendula*; EventId: EvN no 2018230-H; RMNH.INS.46487. • 11 mines; Valperga, Sacro Monte di Belmonte; 45.36688°N, 7.63067°E; alt. 685 m; 01 Oct. 2018; EvN leg.; *B. pendula*; EventId: EvN no 2018238-1H; RMNH.INS.46497.

NETHERLANDS – Gelderland • 1 mine; Ede, Edese Heide, Koeweg; 52.05867°N, 5.69665°E; 16 Sep. 2020; EvN leg.; *B. pendula*; EventId: EvN no 2020064-2H; RMNH.INS.48336. • 6 mines; Ede, Planken Wambuis, Mosselse Pad; 52.07214°N, 5.7576°E; 16 Sep. 2020; EvN leg.; *B. pendula*; EventId: EvN no 2020058-2H; RMNH.INS.48308. • 3 mines; Ugchelen, Leesterheide, t Leesten; 52.16887°N, 5.90794°E; 07 Oct. 2020; EvN leg.; *B. pendula*; EventId: EvN no 2020097-1H; RMNH.INS.48432. • 1 mine; same locality data; *B. pubescens*; EventId: EvN no 2020098-1H; RMNH.INS.48437. • 3 larvae (ethanol, tissue collection, DNA barcoded, slide), 22 mines; Wekerom, De Valouwe, Immenkampweg; 52.08977°N, 5.71459°E; 16 Sep. 2020; EvN leg.; *B. pendula*; EventId: EvN no 2020062-1H/K/M; RMNH.INS.31449–31450, RMNH.INS.48317–48319. • 10 mines (larvae reared); Wekerom, Wekeromse Zand, near Hoge Valksedijk; 52.09188°N, 5.67616°E; 16 Sep. 2020; EvN leg.; *B. pendula*; EventId: EvN no 2020063-1H/K; RMNH.INS.48327–48328. • 4 mines (larva reared); Wolfheze, Wolfhezerbos, Oude Kloosterweg; 51.997°N, 5.79882°E; 07 Oct. 2020; EvN leg.; *B. pendula*; EventId: EvN no 2020100-1H/K; RMNH.INS.48445–48446. – **Limburg** • 1 mine; Epen, Onderste Bos; 50.7657°N, 5.89338°E; 20 Sep. 2020; EvN leg.; *B. pendula*; EventId: EvN no 2020067-2H; RMNH.INS.48342. • 1 mine; Epen, Geuldal, Cottessen; 50.76232°N, 5.93053°E; 20 Sep. 2020; EvN leg.; *B. pendula*; EventId: EvN no 2020068-2H; RMNH.INS.48346. • 1 larva (DNA barcoded, slide), 6 mines; Leudal, Nunhem - Sint Ursula, Zelsterbeek valley; 51.25424°N, 5.9512°E; 21 Sep. 2020; EvN leg.; *B. pubescens*; EventId: EvN no 2020073-1H/M; RMNH.INS.31460, RMNH.INS.48359–48360. • 5 mines; same locality data; *B. pendula*; EventId: EvN no 2020072-1H; RMNH.INS.48357. • 1 larva, 10 mines; Leudal, Sint Elisabeth, 2 km E Heythuysen; 51.24649°N, 5.92678°E; 21 Sep. 2020; EvN leg.; *B. pendula*; EventId: EvN no 2020070-1H/M; RMNH.INS.31458, RMNH.INS.48350–48351. • 4 mines (larva reared); Leudal, Sint Elisabeth, Roggelse Beek valley; 51.25462°N, 5.93057°E; 21 Sep. 2020; EvN leg.; *B. pendula*; EventId: EvN no 2020071-1H/K; RMNH.INS.48354–48355. – **Noord-Brabant** • 14 mines (2 larvae reared); Goirle, Gorp en Roovert - Noord; 51.50795°N, 5.07473°E; 30 Sep. 2020; EvN leg.; *B. pendula*; EventId: EvN no 2020082-1H/K; RMNH.INS.48381–48382. • 2 larvae (ethanol, tissue collection, DNA barcoded, slide), 22 mines (3 larvae reared); Goirle, Gorp en Roovert - Noord; 51.50512°N, 5.08499°E; 30 Sep. 2020; EvN leg.; *B. pendula*; EventId: EvN no 2020083-1H/K/M; RMNH.INS.31465–31466, RMNH.INS.48389–48391. • 22 mines; Goirle, Regte Heide; 51.52008°N, 5.03386°E; 30 Sep. 2020; EvN leg.; *B. pendula*; EventId: EvN no 2020081-1H; RMNH.INS.48377. • 9 mines; Leende, Leenderbos, Parking Strijperpad; 51.35075°N, 5.51628°E; 19 Sep. 2020; EvN leg.; *B. pendula*; EventId: EvN no 2020065-1H; RMNH.INS.48337. • 10 mines; Tilburg, Kaaistoep Oost; 51.54092°N, 5.02876°E; 30 Sep. 2020; EvN leg.; *B. pendula*; EventId: EvN no 2020079-1H; RMNH.INS.48370. • 4 mines; Tilburg, Wilhelminakanaal, East banks; 51.52175°N, 5.14482°E; 30 Sep. 2020; EvN leg.; *B. pendula*; EventId: EvN no 2020084-1H; RMNH.INS.48398. • 2 mines; same locality data; *B. pubescens*; EventId: EvN no 2020085-1H; RMNH.INS.48402. • 2 mines; Tilburg, De Sijsten, Heidebaan; 51.54111°N, 5.00389°E; 30 Sep. 2020; EvN leg.; *B. pendula*; EventId: EvN no 2020080-1H; RMNH.INS.48375. – **Overijssel** • 4 mines; Lemele, Lemelerberg; 52.46178°N, 6.39946°E; 3 Aug. 2022; EvN leg.; *B. pendula*; EventId: EvN no 2022005-1H; RMNH.INS.48842. – **Utrecht** • 13 mines (rearing failed); Leersum, Dartheide; 52.02°N, 5.4083°E; 25 Sep. 2020; Ben van As leg.; *B. pendula*; EventId: EvN no 2020087-K/H; RMNH.INS.48407. • 1 mine; Leusden, Den Treek, Hazenwater; 52.12511°N, 5.37929°E; 10 Sep. 2020; EvN leg.; *B. pubescens*; EventId: EvN no 2020052-5H; RMNH.INS.48278. • 5 mines; Leusden, Den Treek-Henschoten, t Waswater; 52.11789°N, 5.37407°E; 10 Sep. 2020; EvN leg.; *B. pubescens*; EventId: EvN no 2020054-1H; RMNH.INS.48281. • 19 mines; Soest, Korte Duinen S.; 52.15137°N, 5.3261°E; 04 Sep. 2020; EvN leg.; *B. pendula*; EventId: EvN no 2020046-1H; RMNH.INS.48250. • 2 mines; Soest, Korte Duinen S.; 52.15131°N, 5.32578°E; 04 Sep. 2020; EvN leg.; *B. pubescens*; EventId: EvN no 2020047-4H; RMNH.INS.48259. • 1 larva (ethanol, tissue collection), 49 mines; Soest, Korte Duinen S.; 52.15122°N, 5.32729°E; 10 Sep.

2020; EvN leg.; *B. pendula*; EventId: EvN no 2020055-1H/M; RMNH.INS.31444, RMNH.INS. 48288, 48290. • 10 mines; Soest, Korte Duinen S.; 52.15131°N, 5.32675°E; 23 Aug. 2021; EvN leg.; *B. pendula*; EventId: EvN no 2021120-1H/K; RMNH.INS.48692–48693. • 3 larvae (ethanol, tissue collection, DNA barcoded, slide), 25 mines (larvae reared); Soest, Korte Duinen S. edge; 52.15107°N, 5.32399°E; 10 Sep. 2020; EvN leg.; *B. pendula*; EventId: EvN no 2020056-1H/K/M; RMNH.INS.31441–31443, RMNH.INS.48297–48299. • 13 mines; Soest, Korte Duinen S. edge; 52.15112°N, 5.32402°E; 23 Aug. 2021; EvN leg.; *B. pubescens*; EventId: EvN no 2021121-1H/K; RMNH.INS.48696–RMNH.INS.48697. • 9 mines; Soest, Korte Duinen S. edge; 52.15112°N, 5.32402°E; 23 Aug. 2021; EvN leg.; *B. pendula*; EventId: EvN no 2021122-1H/K; RMNH.INS.48699–48700. • 1 larva (DNA barcoded, slide), 8 mines; Soest, Lange Duinen E.; 52.15116°N, 5.30074°E; 04 Sep. 2020; EvN leg.; *B. pendula*; EventId: EvN no 2020049-1H/M; RMNH.INS.31436, RMNH.INS.48264–48265. • 1 larva, 1 mine; Soest, Lange Duinen S.; 52.14687°N, 5.28791°E; 23 Aug. 2021; EvN leg.; *B. pubescens*; EventId: EvN no 2021130-M/H; RMNH.INS.31659, RMNH.INS.48713. • 1 mine; Soest, Op Hees, W border; 52.15582°N, 5.25182°E; 23 Aug. 2021; EvN leg.; *B. pendula*; EventId: EvN no 2021125-H; RMNH.INS.48705. • 3 mines; Soest, Op Hees, W border; 52.15582°N, 5.25182°E; 23 Aug. 2021; EvN leg.; *B. pubescens*; EventId: EvN no 2021126-1H; RMNH.INS.48706. • 6 mines; Soest, Op Hees/ Willem Arntzbos; 52.15152°N, 5.25401°E; 23 Aug. 2021; EvN leg.; *B. pubescens*; EventId: EvN no 2021127-H/K; RMNH.INS.48708–RMNH.INS.48709. • 2 mines; Soest, Hees, Wieksloterweg, Heitje; 52.15885°N, 5.27867°E; 23 Aug. 2021; EvN leg.; *B. pubescens*; EventId: EvN no 2021123-K; RMNH.INS.48704. • 5 mines; Soest, Soesterberg, nr Wildwissel, along railway; 52.14528°N, 5.26222°E; 23 Aug. 2021; EvN leg.; *B. pubescens*; EventId: EvN no 2021128-H/K; RMNH.INS.48710–48711.

POLAND • 5 mines; Mazowieckie, Walendów; 52.08816°N, 20.8445°E; 16 Sep. 2010; V. Lanta leg.; *B. pendula*; RMNH.INS.45444.

RUSSIA—**Irkutsk Oblast** • 1 larva (DNA barcoded, slide), 2 mines; Tulun; 54.60111°N, 100.64°E; alt. 510 m; 22 Aug. 2009; V. Chepinoga leg.; *B. pendula* subsp. *mandshurica*; EventId: Kozlov-3-leaf1; RMNH.INS.29880, RMNH.INS.46693. — **Kaluga Oblast** • 1 mine; Kondrovo Distr., Gorbenki; 54.6589°N, 35.9385°E; 13 Aug. 2013; L.V. Bolshakov leg.; *B. pendula*; RMNH.INS.45634. — **Krasnoyarsk Krai** • 1 larva (DNA barcoded, slide); village Tanzybei, foothill of Sayan Mts; 53.1199°N, 92.9672°E; 17 Jun. 2017; N. Kirichenko leg.; *B. pendula*; EventId: NK-13-17; RMNH.INS.31140. — **Lipetsk Oblast** • 1 mine; Krasnoe Distr., Jablonovo; 52.8318°N, 38.9817°E; 11 Aug. 2014; L.V. Bolshakov leg.; *B. pendula*; RMNH.INS.47960. • 2 mines; Krasnoe Distr., Leski; 52.8729°N, 38.97°E; 15 Jul. 2013; L.V. Bolshakov leg.; *B. pendula*; RMNH.INS.45783. • 1 larva (DNA barcoded, slide), 61 mines; Usman Distr., Usman; 51.983°N, 39.783°E; alt. 165 m; 28 Jul. 2017; V. Zverev leg.; *B. pendula*; RMNH.INS.31160, RMNH.INS.44331, RMNH.INS.44341, RMNH.INS.45010. • 46 mines; same locality data; *B. pubescens*; RMNH.INS. 44337–44338. — **Moscow Oblast** • 1 mine; Serpukhov, Svinenki; 54.9°N, 37.8°E; alt. 130 m; 16 Sep. 2009; M. Brynskikh leg.; *B. pendula*; RMNH.INS.46670. — **Novosibirsk Oblast** • 1 larva (DNA barcoded, slide); Novosibirsk, Central Siberian botanical garden; 54.82°N, 83.10389°E; alt. 155 m; 10 Jul. 2012; N. Kirichenko leg.; *B. pendula*; EventId: CD13121; RMNH.INS.30247. • 7 mines; same locality data; 14 Sep. 2013; N. Kirichenko leg.; *B. pendula*; EventId: NK# 68_12; RMNH.INS.40809, 40810. — **Sverdlovsk Oblast** • 1 mine; Revda; 56.8075°N, 59.3625°E; alt. 375 m; 15 Aug. 2009; E. Belskaya leg.; *B. pubescens*; RMNH.INS.46719. — **Tula Oblast** • 2 mines; Kurkino Distr., Danilovka; 53.5926°N, 38.5499°E; 26 Jul. 2006; L.V. Bolshakov leg.; *B. pendula*; RMNH.INS.45931. • 1 mine; Kurkino Distr., Vodyanoe Pole; 53.6176°N, 38.5766°E; 17 Jul. 2009; L.V. Bolshakov leg.; *B. pendula*; RMNH.INS.45973. • 2 mines; Leninski Distr., Inshinsky, 10 km W. Tula; 54.1436°N, 37.4738°E; 26 Sep. 2009; L.V. Bolshakov leg.; *B. pendula*; RMNH.INS.45976. • 1 mine; Shchyokino Distr., Yasnaya Polyana, 14 km S Tula; 54.0893°N, 57.5101°E; 01 Aug. 2009; L.V. Bolshakov leg.; *B. pendula*; RMNH.INS.46010. — **Ulyanovsk Oblast** • 6 mines; Surskoe Distr., 10 km WNW vill. Lava; 54.55°N, 46.883°E; 07 Jul. 2019; V. Zolotuhin leg.; *B. pubescens*; EventId: VZ19_13-Betula pubescens; RMNH.INS.46845. • 1 mine; Ulyanovsk city; 54.3°N, 48.38°E; 09 Sep. 2002; students Ulyanovsk State Pedag. Univ. leg.; *B. pendula*; RMNH.INS.27861. • 1 larva (DNA barcoded, slide), 82 mines; Ulyanovsk city S., Vinnovka

forest-park; 54.27°N, 48.03°E; Jul.– Aug. 2002; A. Mistchenko leg.; *B. pendula*; slide: EvN3566; RMNH.INS.23566, RMNH.INS.27857–27860. • 4 mines; Ulyanovsk Oblast, Ulyanovsk city S., Vinnovka forest-park; 54.27°N, 48.03°E; 21 Sep. 2002; A. Mistchenko leg.; *B. pendula*; RMNH.INS.27862, RMNH.INS.27866 [the latter was misidentified as *S. betulicola* by van Nieukerken et al. 2004]. • 1 mine; Ulyanovsk city S., Vinnovka forest-park; 54.27°N, 48.03°E; 30 Sep. 2002; A. Mistchenko leg.; *B. pendula*; RMNH.INS.27863. – **Voronezh Oblast** • 1 larva (DNA barcoded, slide), 3 mines; Voronezh; 51.583°N, 39.167°E; alt. 150 m; 28 Aug. 2017; V. Zverev leg.; *B. pubescens*; RMNH.INS.31325, RMNH.INS.46142.

SLOVAKIA • 2 mines; Západoslovenský Kraj, Sekule, 6 km SW Kúty; 48.614°N, 17.009°E; 04 Oct. 1992; EvN leg.; *B. pendula*; EventId: EvN no 92075; RMNH.INS.48289.

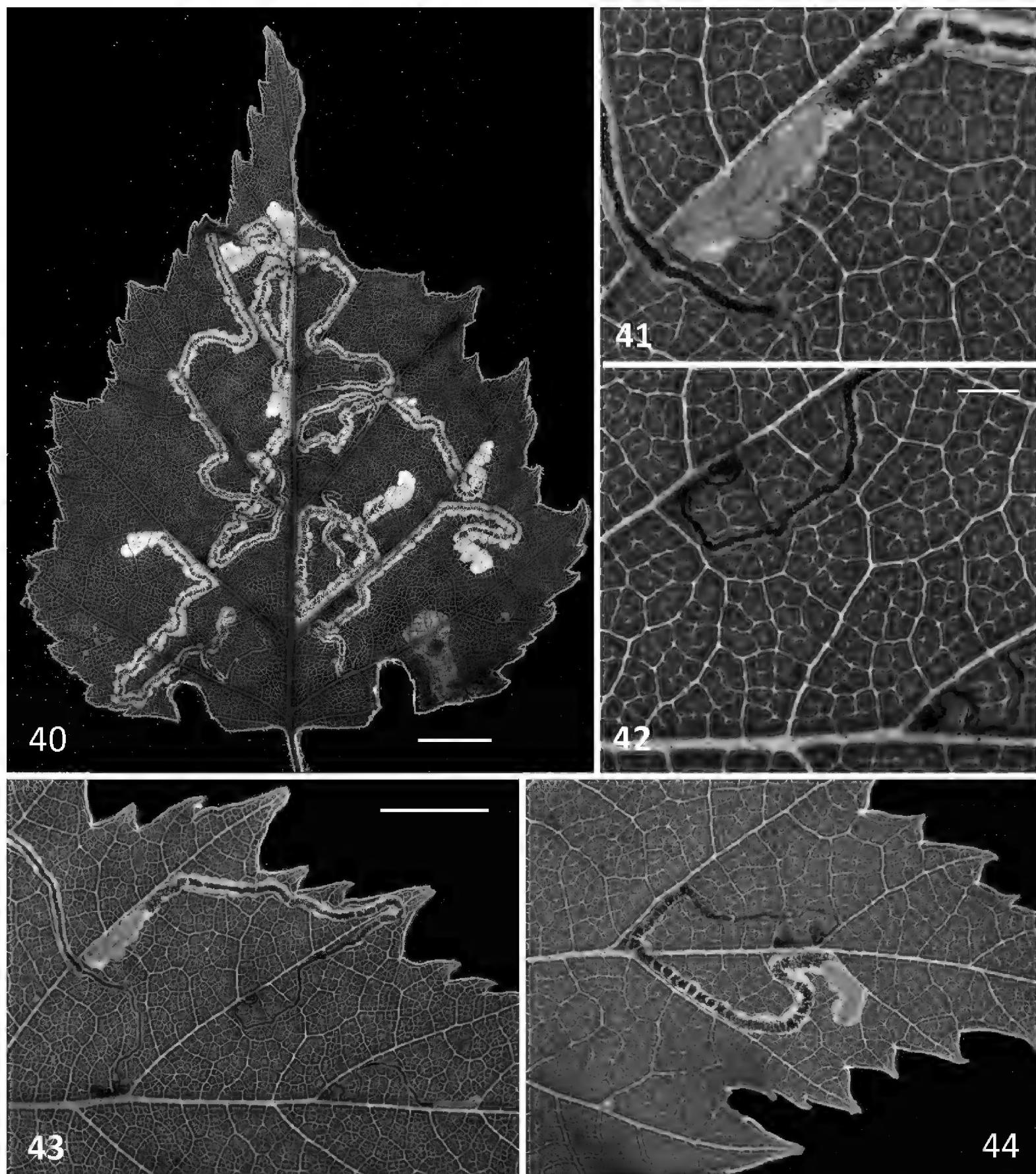
Leafmine diagnostics

Although most leafmines occurring on *Betula* in Europe can be identified from the leafmine pattern and larval characters with several sources (Hering 1957; Pitkin et al. 2019; Edmunds 2022; Ellis 2022), identification of linear or corridor mines is still a challenge, especially now, since *S. naturella* appears to have become widespread, while the two *Stigmella* species normally found on *Alnus* have been recorded on *Betula* several times in more southern parts of Europe. To assist identification, diagnostic notes are provided for all *Stigmella* species occurring on *Betula* in Europe followed by an identification key.

Identification is easiest for either completed, vacated mines, in fresh condition (or dried when fresh), or mines with active larvae in their final instar. Old and withered mines should preferably be left on the tree, only with experience can they sometimes be distinguished. Moreover, mines with dead or parasitised larvae may be more difficult or even impossible to identify, as are mines containing young larvae. It is important to check whether the position of the egg is on the leaf upper- or underside as it is for the position of the exit slit where the larva has left the mine. These characters can only be seen effectively with magnification, at least a loupe in the field is necessary or a stereo microscope in the laboratory. For photographic recording detailed images are needed, and especially photos with back lighting, which shows frass and larva better.

Larvae of Nepticulidae usually are situated in their mines with the ventral side at the leaf upper-side, but all species belonging to “Core *Stigmella*” (Doorenweerd et al. 2016: 279) have the dorsum upwards. This character, often overlooked, is helpful in separating the species belonging to core *Stigmella* (here *S. continuella*, *S. lapponica*, *S. confusella* and *S. tristis*) from the rest. The larval head capsule, especially in the final instar, is longer at the dorsal side than at the ventral side (high magnification needed; see e.g. Gustafsson and van Nieukerken 1990), dorsally the paired brains may be visible (e.g. Fig. 69), no other ganglia, whereas in species with venter upwards often the ventral nerve chord is visible (e.g. Fig. 41), but this may be obsolete, and in *S. naturella* only the suboesophageal ganglion is visible (Figs 23, 24).

Stigmella naturella (Klimesch, 1936) (Figs 18–27, 29–34). Egg: on leaf under- or upperside, usually away from major veins, rarely against a vein, more often in the area near the margin. Exit: leaf upperside. Larva: venter upwards, pale whitish, with distinct brown circular suboesophageal ganglion, but no other ventral ganglia visible. Early mine: starts directly away from egg, sometimes with single bend around egg; early mine often appearing green as larva eats only sponge parenchyma. Later mine: rather variable, rarely very straight, but sometimes with straight parts; frass often rather narrow, but can be much wider and forming clumps.



Figures 40–44. *Stigmella betulicola*, leafmines **40**. 7 vacated mines, France, Le Mans, 7 Oct. 2017, *Betula pubescens*, 7 adults emerged Mar. 2018, EvN no. 2017150-K; **41–44**. Occupied mines, The Netherlands, Goirle, 30 Sep. 2020, *B. pendula*, EvN no. 2020083-2; **41**. Detail of larva; **42**. Details of coiled mine start. Scale bars: 1 mm (to 41 and 42); 5 mm (43 and 44 on same scale).

Occurrence: usually on mature trees, occasionally on juvenile trees, rarely more than one or two mines per leaf. Prefers dryer habitats in open forests and *Betula pendula*, but can be found in many other habitats as well. Larvae of second generation occur from August, often in low numbers.

Note: mines with upperside egg and/or green early part are easy to recognise, vacated mines without these characters may be difficult to separate especially from those of *S. confusella*, but mine of *S. naturella* is usually narrower (final larval chamber 0.9–1.4 mm wide) and shorter (length 22–53 mm, small overlap with *S. confusella*) and frass appears more broken. Some isolated mines may be unidentifiable, so studying a series of mines is best for a certain identification.

Stigmella betulicola (Stainton, 1856) (Figs 40–44). Egg: on leaf underside, against a major vein. Exit: leaf underside. Larva: venter upwards, deeply yellow, with chain of ventral ganglia clearly visible. Early mine: starts contorted with close coils in a very confined area (Fig. 42), never green. Later mine: rather variable, frass width variable, between 1/3 and 3/4 mine width, sometimes filling early mine completely, mine rather long or shorter in thicker leaves.

Occurrence: most frequent on low growth, seedlings, juvenile trees, often gregarious with many mines on one leaf.

Note: mines of *S. luteella* are often mistaken for *S. betulicola* when the green part of the mine is absent. The larger contorted part and small differences in frass deposition may help if no larva is present, but some mines remain unidentifiable. Mines of *S. glutinosae* may be very similar to *S. betulicola*, but do not have coils at the start of the mine.

Stigmella luteella (Stainton, 1857) (Figs 45–52). Egg: on leaf underside (rarely on upperside), against a major vein. Exit: leaf underside. Larva: venter upwards, pale yellow, ventral ganglia hardly or not visible. Early mine: starts with a distinctly contorted part (Fig. 52), area larger than in *betulicola*; frequently the early part of the mine is in the spongy parenchyma and therefore appearing green from above. Later mine: rather variable, frass either in a very thin line or the line is broader (up to 3/4 the width of the mine) and the frass line is broken, mine rather long, shorter in thicker leaves; sides of mine often scalloped.

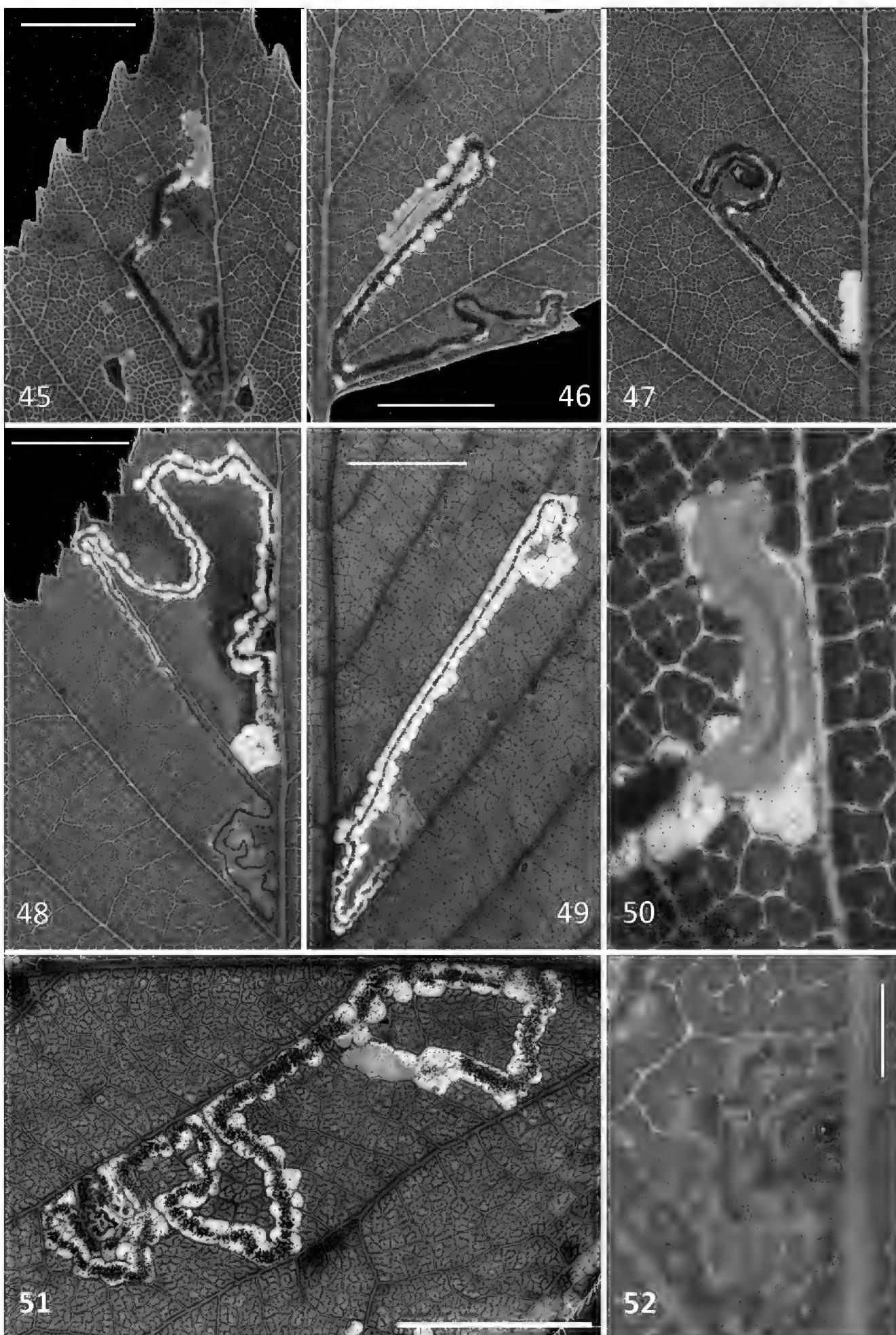
Occurrence: usually on mature trees, occurring later in the season than most *Stigmella* species, frequently found still feeding in green islands in fallen leaves in October–November. Rarely gregarious.

Note: mines of *S. luteella* are often mistaken for *S. betulicola* when the green part of the mine is absent, especially in northern Europe. The larger contorted part and small differences in frass deposition may help identification if no larva is present, but some mines will remain unidentifiable.

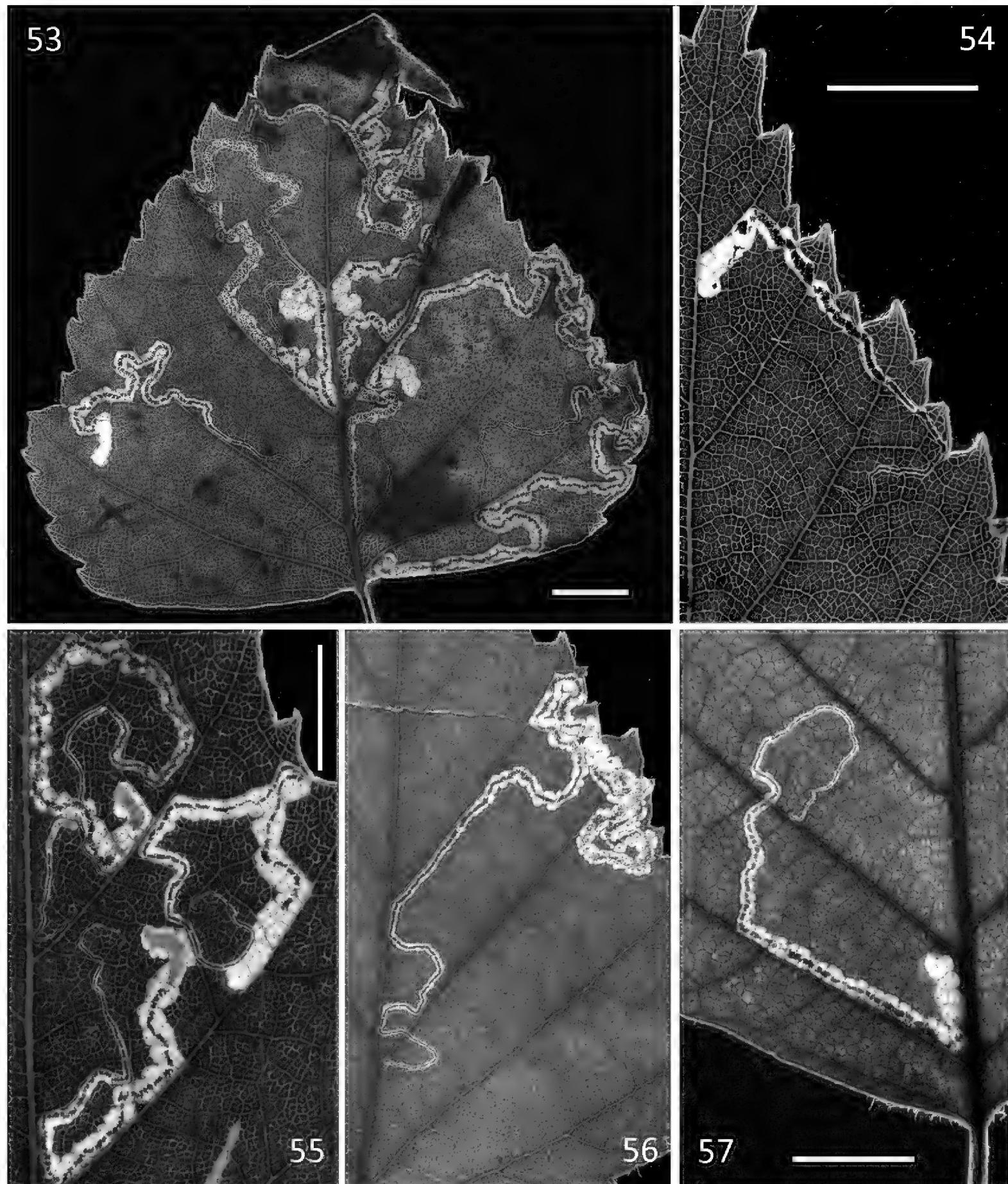
Stigmella glutinosae (Stainton, 1858) (Figs 53–57). Egg: usually on leaf underside, against a major vein, in some cases on upperside (about 20% of 51 mines examined, but all upperside eggs were in one sample). Exit: usually leaf underside, in some cases on upperside. Larva: venter upwards, pale yellow, ventral ganglia hardly or not visible. Early mine: runs straight away from egg. Later mine: rather variable, frass either in a very thin line, or a broader line with frass dispersed, and width up to 2/3 of the mine, mine rather short, total length 23.2–41.4 mm (34.5 ± 6.4, 6), final larval chamber 1.0–1.4 mm wide.

Occurrence: when on *Betula* often on seedlings and juvenile trees, but also on mature trees. Occasionally gregarious (Fig. 53). More frequent on *Alnus*, but in southern parts of Russia and in France several times recorded on *Betula*, proven by rearing and DNA barcodes. Some leafmines from Germany (Fig. 57) and the Netherlands probably also belong to *glutinosae*, but independent confirmation is lacking.

Note: mines of *S. glutinosae* may resemble those of *naturella*, but the egg position on a vein and larval exit on underside usually separate the two, as does the green early mine in many *naturella*. Some mines remain unidentifiable. Some of the mines from Ulyanovsk figured as *S. naturella* by van Nieukerken et al. (2004: fig. 10) fit *S. glutinosae* better, suggesting that the mine sample was a



Figures 45–52. *Stigmella luteella*, leafmines **45–47**. 2 Occupied mines and one vacated mine, The Netherlands, Ede, 16 Sep. 2020, *Betula pubescens*, EvN no 2020058-1K; **48**. Vacated mine, The Netherlands, Wekerom, 16 Sep. 2020, *B. pendula*, EvN no 2020062-2; **49**. Vacated mine, Germany, Hamburg, 28 Sep. 1932, *B. utilis*, published as *Nepticula naturnella* by Buhr (1940b: 229); **50**. detail of larva in Fig. 45; **51**. mine with dead larva, barcoded, Russia, Karelia Rep., Nadvoitsy, 26 Aug. 2012, *B. pubescens*, RMNH.INS.29973; **52**. data as Fig. 48, early part of mine and egg, leaf underside. Scale bars: 5 mm (45–49, 51); 1 mm (52); no scale for 50.



Figures 53–57. *Stigmella glutinosae*, leafmines on *Betula*, confirmed by DNA barcoding, except 57. **53.** France, Le Mans, 7 Oct. 2017, *B. pubescens*, 6 mines, 4♂ 1♀ emerged, left mine, near cross, incomplete, larva taken for barcoding, EvN no 2017150-3K/M; **54.** France, Villeneuve-sur-Cher, 30 Jul. 2009, larva taken from mine, *B. pendula*, EvN no 2009039-M; **55.** Russia, Voronezh, 28.viii.2017, *B. pendula*, dried mines with larvae, larva taken from right mine, RMNH.INS.31158; **56.** Russia, Lipetsk Obl., Osman, 28 Aug. 2017, *B. pendula*, RMNH.INS.31159; **57.** Vacated mine, Germany, Berlin, Botanischer Garten, 17 Aug. 1936, *B. papyrifera* (as *B. excelsa*), published as *Nepticula naturnella* by Buhr (1940b: 229). Scale bars: 5 mm (55–57 on same scale).

mixture of the two. It is highly likely that the leafmine reported as *S. confusella* from Ukraine, the Crimea by Navickaitė et al. (2014) also belongs to *S. glutinosae*.

Stigmella alnetella (Stainton, 1858) (Figs 58, 59). Only two mines on *Betula* are available that are proven by DNA barcodes, to be from *S. alnetella*. Egg: on leaf underside, against a major vein. Exit: leaf underside. Larva: venter upwards, pale yellow, ventral ganglia hardly or not visible. Early mine: slightly coiled. Later mine: with frass coiled, in a rather broad line in both the mines examined. Probably more variable, as in the leafmines on *Alnus*.

Occurrence: both mines on *Betula* were on mature trees. Common on *Alnus*, the two larvae bar-coded from *Betula* were from Italy; reared once in Sweden (Johansson and Nielsen 1990).

Note: Considering the difficulty of separating mines of *S. alnetella* from those of *glutinosae* on *Alnus*, we expect to experience the same difficulty on *Betula*. The two mines examined resemble somewhat those of *S. sakhalinella*, but distinguishing features are: egg on vein, early mine with narrow linear frass and exit on leaf underside. These two Italian mines were found amongst a large number of vacated mines resembling those of *S. glutinosae*, that could belong to either species, but are tentatively identified as *S. glutinosae*.

Stigmella sakhalinella Puplesis, 1984 (in older European literature under the name *S. distinguenda* auct.) (Figs 60–63). Egg: usually on leaf underside, but in several cases on leaf upperside, most frequently near leaf margin, but other positions over the whole leaf have been observed. Exit: leaf upperside. Larva: venter upwards, dark yellow, ventral ganglia clearly visible. Early mine: starts rather contorted, filled with dark frass. Later mine: usually somewhat contorted, or following leaf margin, frass black, coiled, usually almost filling width of mine, leaving narrow borders; occasionally the frass line is narrower, but still coiled (Fig. 61).

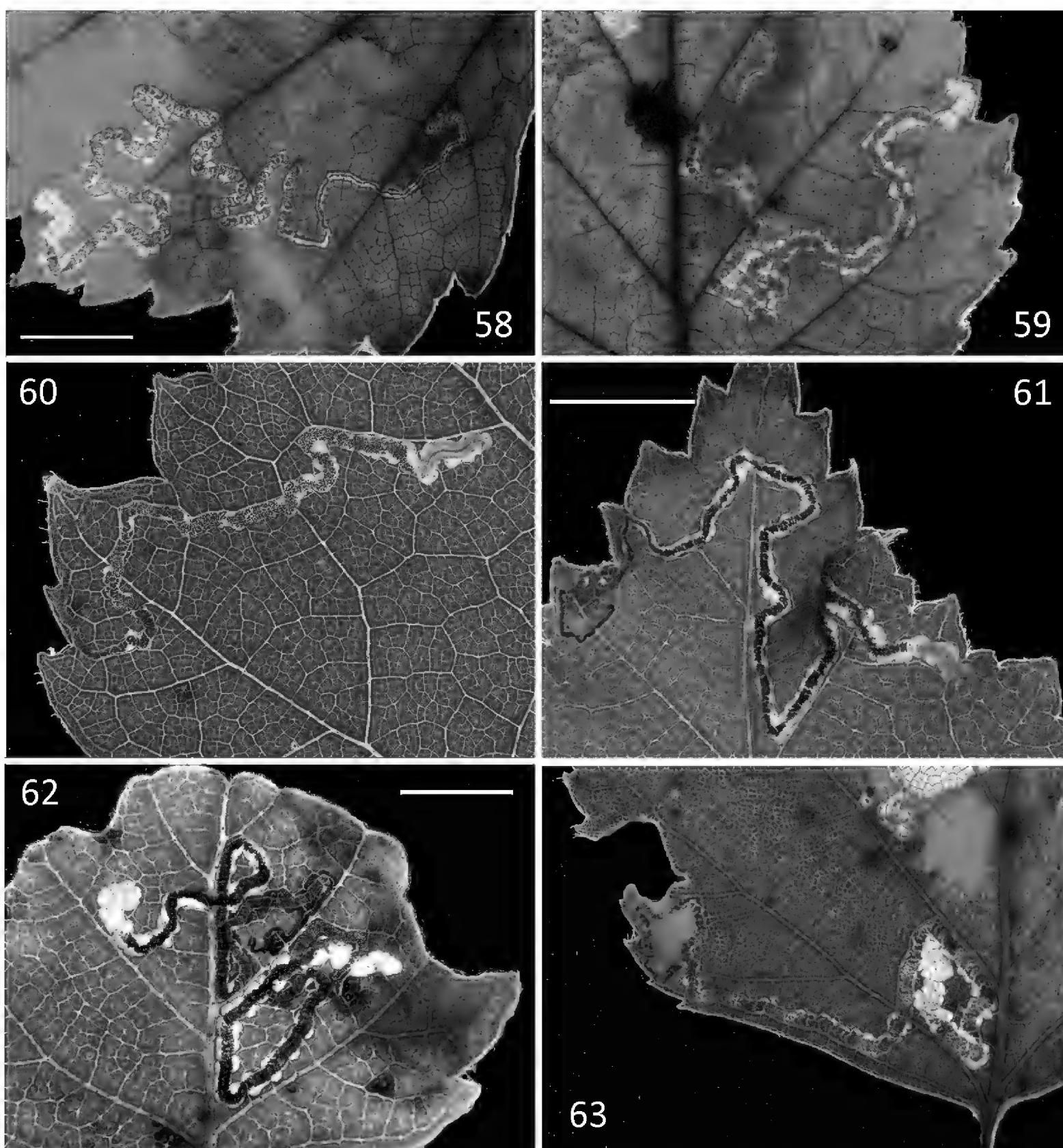
Occurrence: usually on mature trees, but also on juvenile trees, occasionally gregarious.

Note: mine unmistakeable, although *S. alnetella* when rarely on *Betula* has some resemblance in the second part of the mine. Young mines sometimes confused with *S. betulicola*.

Stigmella confusella (Wood & Walsingham, 1894) (Figs 64–69). Egg: on leaf underside, usually close to a vein. Exit: leaf upperside. Larva: dorsum upwards, greenish whitish, the bilobed brain clearly visible from upper side, differing from the (ventral) circular suboesophageal ganglion in *S. naturnella*, no other ganglia visible from above. Mine: often with long straight stretches, following veins partly, occasionally partly more contorted (as in Figs 64, 65), especially at start; overall the mine has an angular appearance; frass throughout in a narrow central line, often continuous, only partly broken in later part of mine.

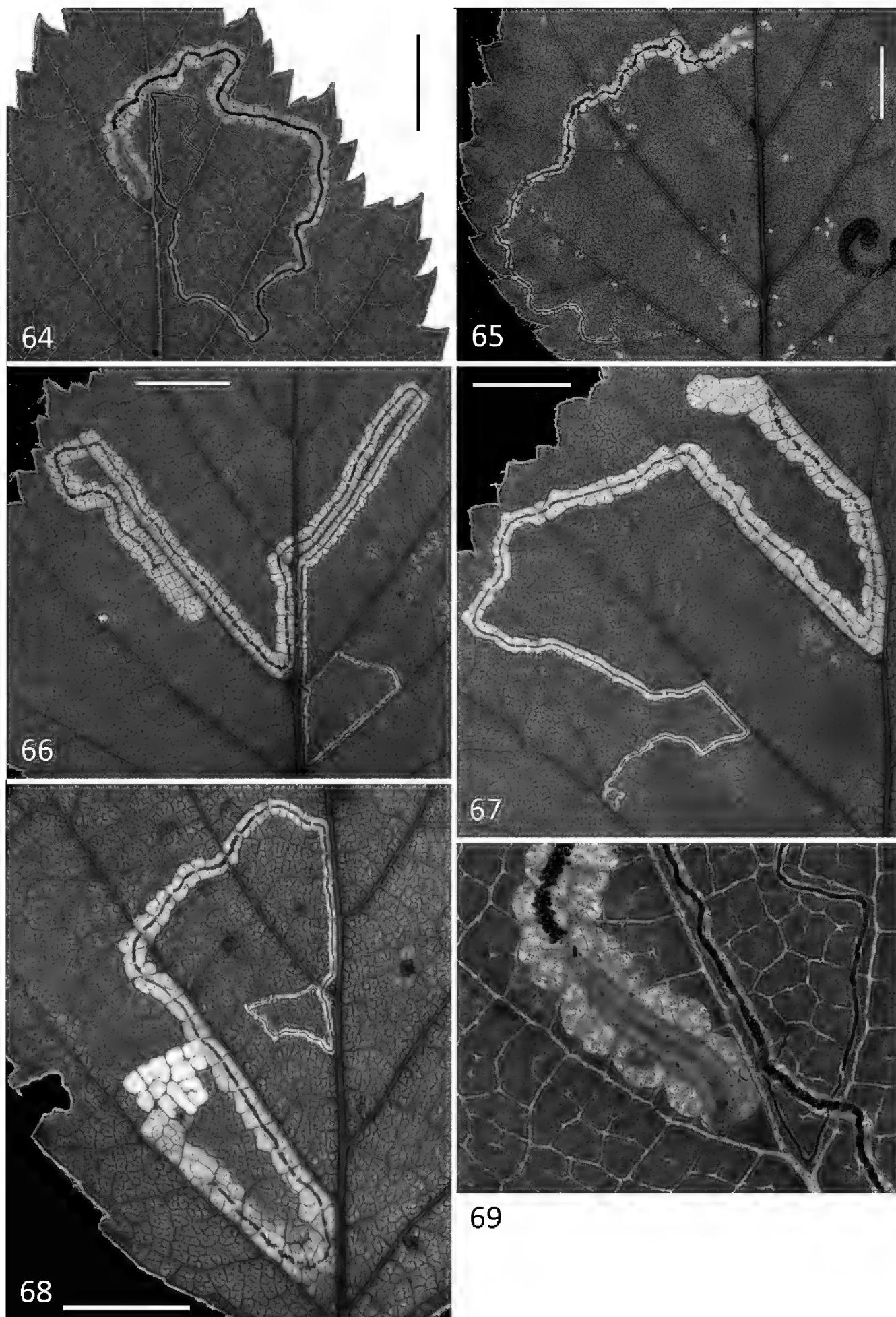
Occurrence: usually on mature trees, rarely with more than two mines per leaf. Prefers *B. pubescens* in moist habitats. Univoltine, usually occurring later than *S. lapponica*.

Note: mine most similar to *S. lapponica*, but the early frass of that species always separates the two. Less typical mines may be confused with *S. naturnella*, but the species are not often found together and *S. confusella* has a considerably longer mine: 41–91 mm (68.9 mm ± 15.6, n=12), with only a small overlap with *S. naturnella*. Also, the final larval chamber is wider: 1.3–2.0 mm (1.6 ± 0.2, n=12), and usually straight, whereas that of *S. naturnella* is often buckled. However, some unfinished mines (without distinct larval remains) in areas where both species occur may be inseparable. Vacated mines of *Lyonetia clerkella* are sometimes mistaken for *S. confusella*, especially where photographs are used for determination, but the extreme length of the mine, its sinuous condition and the absence of a visible egg are diagnostic.



Figures 58–63. **58, 59.** *Stigmella alnetella*, vacated leafmines on *Betula*, confirmed by DNA barcoding, Italy, Roma, Manziano, 17 Sep. 2005, *B. pendula*, EvN no 2005115-3M **60–63.** *Stigmella sakhalinella*, leafmines. **60.** Occupied mine, Netherlands, Soest, 23 Aug. 2021, *B. pendula*, EvN no 2021122-2K; **61.** Occupied mine, Netherlands, Wassenaar, 10 Oct. 2018, *B. pubescens*, EvN no 2018263-2; **62.** Vacated mine, Netherlands, Wassenaar, Meijendel, 11 Oct. 2007, *B. pubescens*, EvN no 2007122-1M; **63.** Vacated mine, Finland, Helsinki, Ojakkala, 1 Sep. 2017, *B. pendula*, RMNH.INS.44352. Scale bars: 5 mm (58 & 59, 60 & 61 and 62 & 63 each on same scale).

Stigmella lapponica (Wocke, 1862) (Figs 70–72). Egg: on leaf underside, usually close to a vein. Exit: leaf upperside. Larva: dorsum upwards, greenish whitish, the bilobed brain clearly visible from upper side, differing from the circular suboesophageal ganglion in *S. naturella*, no other ganglia visible from above. Early mine (made by first 3 instars) filled entirely with green or brown



Figures 64–69. *Stigmella confusella*, leafmines **64**. Occupied mine, Netherlands, Leidschendam, 11 Aug. 2013, *Betula pubescens*, EvN no 2013098-3; **65**. Occupied mine, dried with larva (barcoded), Russia, St. Petersburg, 1 Jul. 2016, *Betula* sp., RMNH.INS.31461; **66**. Vacated mine, Netherlands, Goirle, 12 Sep. 1982, *B. pubescens*, VU no 82417; **67**. Vacated mine, Norway, Stryn, Kjenndalen, 28 Jul. 2000, *Betula* sp., EvN no 2000115-1H; **68**. Vacated mine, Finland, Harjavalta, 14 Sep. 2009, *B. pendula* **69**. Detail larva of Fig. 64. Scale bars: 5 mm.

frass, in last instar frass arranged in a narrow central line, often continuous, only partly broken in later part of mine. Mine: often with long straight stretches, partly following veins, occasionally rather more contorted, the mine has an angular appearance.

Occurrence: usually on mature trees, rarely with more than two mines per leaf. Prefers *B. pubescens* in moist habitats, occurs earlier than *S. confusella*, univoltine.

Note: unmistakeable by the aberrant early frass. In Nordic mines (northern Fennoscandia, Russia) the frass in the early part differs still from the second part, but often less conspicuously than in more southern populations. Otherwise the same diagnostic characters as in *S. confusella* apply.

Stigmella continuella (Stainton, 1856) (Figs 73, 74). Egg: on leaf underside, almost always on midrib. Exit: leaf upperside. Larva: dorsum upwards, yellow, but in mine often appearing green, no ganglia visible from upper side. Early mine a narrow gallery, much contorted in a zigzag fashion, with windings usually lying against each other, in some cases the windings more separate; earliest part sometimes with narrow linear frass for about 1 mm, later filled with brown frass, early mine forming a distinct brown spot on the leaf, and the leaf tissue between the windings turning brown; later mine a long and rather broad gallery, may follow veins and sometimes angular, filled with green frass pellets, often coiled, arranged in zigzags, frass green when fresh and then almost inseparable from green tissue of leaf, later turning brown.

Occurrence: regularly on seedlings and juvenile trees, but also on mature trees, sometimes with more than two mines per leaf. No host preference, in various habitats, but common in heathland.

Note: unmistakeable from the brown blot at the start and the green frass, which completely fills the mine.

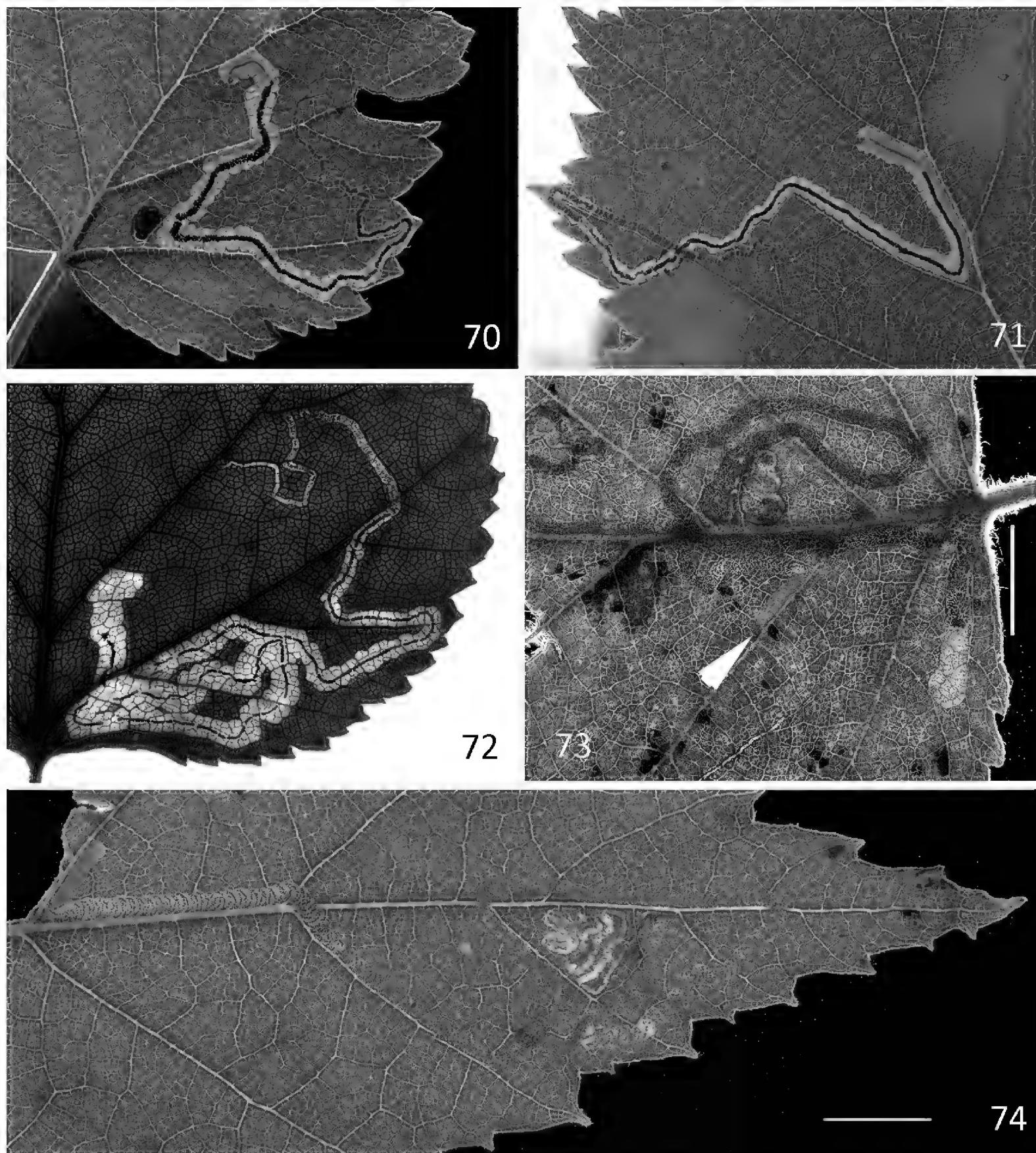
Other linear miners on *Betula*

Stigmella tristis (Wocke, 1862) is an arctic species, confined to *Betula nana* and unlikely to occur sympatrically with *S. naturella*. It is the only other *Betula* mining *Stigmella* species with the egg on leaf upperside (Johansson and Nielsen 1990).

Mines of *Lyonetia clerkella* are often confused with *Stigmella* mines. The extremely long and narrow mines run through the leaves independent of the veins or leaf margins; frass deposited as a broken, central line of variable width. There is no eggshell on the leaf, but an oviposition scar, the larva is very long, with conspicuously constricted segments and distinct legs, visible from the leaf upperside as six black dots. Vacated mines have a very long final chamber without frass. Often on young leaves, seedlings, juvenile trees. Apart from *Betula* also common on Rosaceae trees.

Bucculatrix demaryella (Duponchel, 1840). Regularly confused with young mines of *Stigmella* species, usually *S. luteella*. Egg on leaf underside. Mine is usually short (up to 1 cm), but may be considerably longer in thinner leaves, always starting on the midrib or a larger vein, in a vein angle; usually with blackish frass in a broad line or filling the mine. Larva leaves the mine early, later feeding externally, causing windows on leaf underside. Larval chamber relatively long, three times as long as wide, often bent. The presence of small silken moulting cocoons of young larvae on the leaf are a sign of *Bucculatrix* mines.

Other linear mines are rather different and easier to identify with online keys (Ellis 2022), e.g. the dipteran *Agromyza alnibetulae*, the weevil *Anoplus plantaris* (Naezén, 1794). The early linear



Figures 70–74. *Stigmella lapponica*, leafmines 70. Occupied mine, England, Copley, North Dean wood, 7 Jun. 2018, *B. pubescens*, photo Charlie Streets; 71. Occupied mine, Netherlands, Noordhollands Duinreservaat, 15 Jun. 2018, *Betula* spec., photo Wouter Bol; 72. Vacated mine, Portugal, NP Gerez, 7 Jul. 1980, *B. pubescens*. 73, 74. *Stigmella continuella* 73. Vacated and occupied mine (larva arrowed), Netherlands, Afferden, 24 Sep. 2008, *B. pubescens*, EvN no 2008107-1K; 74. Occupied mine, Netherlands, Wekerom, 16 Sep. 2020, *B. pendula*, EvN no 2020062-4K. Scale bars: 5 mm; no scales available for Figs 70–72.

mines of *Eriocrania sparrmannella* (Bosc, 1791), *E. salopiella* (Stainton, 1854) and *Phylloporia bistrigella* (Haworth, 1828) are sometimes confused with *Stigmella* mines before the blotch part is formed.

Key to mines of *Stigmella* on *Betula* in Europe

- 1 Mine almost completely filled with dispersed frass in distinct coils (“zigzag”), sometimes leaving narrow white margins (Figs 58–63, 73, 74).....**2**
- Mine with frass in a central line of variable thickness, at least in second half of mine, may be broken, and filling up to two thirds of mine width, but never in coils**4**
- 2 Frass in fresh mines green, filling the width of the mine, rendering it almost invisible, later frass turning brown. Early mine narrow brown and much contorted, forming a brown blot (Figs 73, 74). Egg always underside, usually on or near midrib. Larva with dorsum upwards, no ganglia visible.....*S. continuella*
- Frass in fresh mines brown to black, usually leaving narrow white margins. Early mine usually blackish, with few or no coils. Egg position variable, usually underside, sometimes upperside. Larva with venter upwards.....**3**
- 3 Egg away from midrib, anywhere in leaf, often near margin. Exit slit on leaf upperside. Larva deep yellow with conspicuous chain of ganglia visible (Figs 60–63)*S. sakhalinella*
- Egg against midrib or another major vein. Exit slit usually on leaf underside. Larva pale yellow, ganglia not or hardly visible. Rare on *Betula* (Figs 58, 59)*S. alnetella*
- 4 Early mine completely filled with green or sometimes brown frass, later mine angular with narrow central line of frass, the change in frass deposition is abrupt, complete mine long (Figs 70–72). Exit slit on leaf upperside, egg on underside. Larva with dorsum upwards*S. lapponica*
- Early mine may be filled with frass, but without abrupt change between early and later parts of mine, or with narrow frass line. Mine length, exit slit and egg position variable.....**5**
- 5 Egg on leaf upperside**6**
- Egg on leaf underside**8**
- 6 Leafmine on *Betula nana* in northern Europe, mine rather short*S. tristis*
- Leafmine on other species of *Betula*, mine rather long**7**
- 7 Egg anywhere on leaf, but usually away from major veins. Early mine often on underside, appearing green. Exit slit on leaf upperside. Larva pale whitish, with distinct circular suboesophageal ganglion, but no other ventral ganglia visible*S. naturella*
- Egg against midrib or another major vein. Early mine never green. Exit slit usually on leaf underside. Larva pale yellow, ganglia not or hardly visible, but prothorax with square brown plate. Occasionally on *Betula*, common in some places (Figs 53–57)*S. glutinosae*
- 8 Early mine contorted in a small area. Egg against midrib or another major vein. Exit slit on leaf underside. Larva with venter upwards.....**9**
- Early mine running away from egg, not contorted, sometimes with a bend around it. Egg position variable. Exit slit variable. Larva with venter or dorsum upwards**10**
- 9 Early mine usually conspicuously contorted, and often appearing green. Sides of mine often scalloped, scallops usually free of frass. Larva pale yellow, without visible ganglia. Usually on trees, not on seedlings (Figs 45–52)*S. luteella*
- Early mine briefly tightly contorted, never green. Sides of mine rather straight. Larva deep yellow with conspicuous chain of ganglia. Mines often gregarious on seedlings or saplings, rarely on trees (Figs 40–44)*S. betulicola*
- 10 Egg usually away from major veins. Early part of mine may be green or not. Mine not very long (length 22–53 mm), not particularly angular, frass central, of variable thickness; width of final larval chamber 0.9–1.4 mm. Exit slit on upperside. Larva with venter up-

- wards, pale whitish, with distinct circular suboesophageal ganglion, but no other ventral ganglia visible..... *S. naturnella*
- Egg against midrib or another major vein. Early mine never green. Mine rather short (23–41 mm), somewhat angular; width of final larval chamber 1.0–1.4 mm. Exit slit on leaf underside, exceptionally on upperside. Larva with venter upwards, pale yellow, ganglia not or hardly visible, prothorax with square brown plate. Occasionally on *Betula*, common in some places (Figs 53–57)..... *S. glutinosae*
- Egg usually close to a vein. Early mine never green. Mine very long (41–91 mm), usually distinctly angular, with long parts following veins; width of final larval chamber 1.3–2.0 mm. Exit slit on leaf upperside. Larva with dorsum upwards, greenish whitish, the bilobed brain clearly visible from upper side (Figs 64–69)..... *S. confusella*

History of distribution and spread of *Stigmella naturnella*

The original specimens were collected in 1934 and 1935 around the villages of Naturno and Stava in South Tyrol (Italy, prov. Bolzano), where the mines were reported as common, but with few larvae (Klimesch 1936). A few years later Joseph Klimesch collected the species in the Trento region (Klimesch 1948, 1951). Here we report that the species was still common in the Naturno area in 1983 and 1985 (collected by J.J. Boomsma), and in Bolzano province in 2005. Hugo Skala, who was in contact with Klimesch, soon reported more records of this species from Austria, Germany and Czechia (Skala 1937, 1939), but all were based on leafmines alone, without confirmation from reared specimens, which made Klimesch (1948) reluctant to accept these records. The oldest of these records were leafmines collected by Albert Wörz from the Stuttgart area, Württemberg, Germany, in 1935. Later Wörz (1958) repeated these records in detail. Wörz cited Klimesch's opinion on these mines as “höchstwahrscheinlich” (“most likely”). Buhr (1940a, b) reported leafmines of this species, all identified by Skala, from various places in Germany, especially Berlin (botanical garden) and Mecklenburg. These old records have never been re-evaluated after the original publications. Hering (1957) did not cite them, but the Stuttgart records were cited in the German checklists, albeit with doubts in the second edition (Gaedike and Heinicke 1999; Gaedike et al. 2017). I have been able to study most of these leafmines; the majority of Buhr's leafmines from Berlin are still available in his leafmine collection (Herbarium Hausknecht, Jena) and Wörz's leafmines are available in his collection in Stuttgart. Buhr's mines were re-identified by me as belonging to respectively *Stigmella cf glutinosae* and *S. luteella*, but Wörz's leafmines (six in total) from the Willdpark in Stuttgart and Lemberg were indeed correctly identified as *S. naturnella*.

The old record from Czechia in 1937, from Mladé Buky (Jungbuch) (Skala 1939; Haase 1942), also identified by Skala, was given a question mark by Haase and the remark hier muß das Zuchtergebnis erst volle Gewißheit bringen [here must the rearing results provide certainty]. The identity of this record therefore remains uncertain, but is not impossible that it is of *S. naturnella*.

The only other old record that has been confirmed was from Austria, Linz, Bauernberg (Botanical Garden), from mines collected by Skala in 1936 (Skala 1937). Two of his leafmines are housed in the collection of Rebel in the Vienna Museum, of which detailed published photographs show enough detail to consider them as correctly identified (Lödl and Gaal-Haszler 2010) (although it is unfortunate that no photos with back lightning were made); Klimesch (1990) found the species here again in the 1970s, and we have some duplicate mines in RMNH. Karl Burmann also found the species in Innsbruck in 1940 (Hartig 1964), and again in 1950 and 1960. For these we have no confirmations, but they are probably correct.

After the early findings, very little information became available for *S. naturella* for many years. An unpublished record shows that it was present in Czechia, Moravia in 1961, mines collected by H. Zavřel, present in the Hering Herbarium (NHMUK). The next published record was from Hungary in 1968 (Szőcs 1971, 1973), so far the only Hungarian record. It took 20 years for the next published records to be made from Czechia and Slovakia (Laštůvka and Laštůvka 1991; Laštůvka et al. 1992), although the species had meanwhile been found again in 1982 in Austria, in Vorarlberg (<https://www.gbif.org/occurrence/99543229>). I found leafmines of the species in 1983 in Croatia, but at that time I did not recognise them and identified these as *S. betulicola*.

Meanwhile, the species was discovered as *Astigmella dissona* in Far East Russia in the early 1980s (Puplesis 1984a, b). Only much later was it shown that *S. naturella* is the same species, although the synonymy was already suggested by van Nieukerken (1986b). It was subsequently also found in European Russia, with the earliest record from 1992 (van Nieukerken et al. 2004, 2023 in prep).

More records were published from Austria and Czechia (Huemer 1996; Huemer and Wieser 1996; Liška et al. 2000; Laštůvka and Marek 2002; Šefrová 2005; Šumpich 2011, 2017; Wieser 2012), the first record in Switzerland was in 2005 (Kopp 2010) and we here report the first record from Ukraine in 2009.

Up to the early 2000s, most records were within a limited area, Alpine valleys and warmer areas in southern Germany, Czechia, Slovakia and Hungary, and further east throughout Russia (Dubatolov 2007; Bolshakov et al. 2008; van Nieukerken and Sinev 2019; van Nieukerken et al. 2023 in prep). My new recordings of the species in the western Alps of France and Piemonte in 2018 still largely fit this picture. Surprising new records, however, have come from much farther northwards, first from Poland in 2010 (new record of mines from Walendów) and 2011 (Baran 2013), then Germany, Sachsen in 2014 (new record of mines from Pirna), in the Oberlausitz in 2015 and 2017 and in Bavaria in 2017 and 2018 (Guggemoos et al. 2018; Segerer et al. 2019). It was earlier found again in Baden-Württemberg by Willem Ellis and mistaken for *S. luteella* as shown by leafmines in RMNH, collected 28 September 2001 (Fig. 32). In October 2017 I found many leafmines in Central France near Le Mans (Sarthe), a first record for that country; in 2018 independently Mikhail Kozlov and I collected mines in the French Alps, in Savoie.

The earliest indications for an expansion into Belgium and the Netherlands are online observations from 2017, in March and April Guus Dekker observed adults in the Netherlands, Noord-Brabant (Table 1), in August larvae and mines were observed in Belgium, Limburg, Zwarte Beek – Bakel by Carina van Steenwinkel, originally identified as *S. confusella* (<https://waarnemingen.be/observation/142508204/>, see also Ellis 2022) and in October in the Netherlands, Noord-Brabant, near Ossendrecht, originally identified as *S. luteella*. The identity of these and subsequent online records as *S. naturella* was first recognised by me in autumn 2020. In 2018 and 2019 most records were still from Belgium, but in 2020 *S. naturella* appeared to be common in the southern half of the Netherlands, where it was recorded in the provinces Limburg, Noord-Brabant, Utrecht, Noord-Holland (only area near Hilversum) and Gelderland, the Veluwe. In the last province I was unable to find any mines of *S. naturella* in the Veluwe area north of highway A1 (four sites visited in 2020), whereas it was common in southern parts of the Veluwe, a sandy area of forests, heathlands and sand dunes. Yet in the area around Leiden and Wassenaar (Zuid-Holland) *S. naturella* was still absent. The online observations fit this pattern. In 2021 the species was observed more northerly in the province of Flevoland (<https://waarneming.nl/observation/228044436/>),

confirmed again in 2022. In 2022 it was also found in the coastal dunes of Zeeland (Schouwen) and the northernmost records come from the province of Overijssel. More northern records along the coast (Noord-Holland) remain uncertain, these are vacated mines that also may belong to *S. glutinosae*. In Belgium observations originate from the following provinces: Antwerpen, Brussel, Hainaut, Limburg, Oost-Vlaanderen, Vlaams-Brabant and West-Vlaanderen.

Rechecking mines of other *Betula* feeding *Stigmella* in the rich leafmine collections of RMNH did not reveal any older misidentified mines of *S. naturnella* in the Netherlands.

In 2020 *S. naturnella* was also found in Saarland, and in 2021 and 2022 in Nordrhein-Westfalen in Germany, near Hövelhof.

Discussion

Sudden spread?

Stigmella naturnella suddenly appeared in Belgium and the Netherlands after 2017, which can be regarded as a genuine expansion. Leafminers and particularly Nepticulidae had been studied and collected intensely in the Netherlands since the late 1970s, first in our research group at the Free University, including ecological research into *Betula* miners (Boomsma et al. 1987). Later, many volunteers collected data of leafminers all over the Netherlands, especially encouraged by the appearance of the leafmine identification website developed in the early 2000s by Ellis (2022). Furthermore observation websites have led to an enormous increase of the collection/observation effort. Many of the collected leafmines of our research group between 1978 and 1985 are preserved in the RMNH collections, as well as the material collected later by Willem Ellis and collaborators from the former Zoological Museum of Amsterdam. The *Betula* mining *Stigmella* in this large collection have been re-examined by me, resulting in just a few overlooked *S. naturnella* records being cited here (from Croatia and southern Germany), but none from the Netherlands or Belgium.

The situation in other European countries is less clear: there has for instance been hardly a tradition of leafmine collecting and study in France, the few records of leafmines on *Betula* made before the faunal revision (van Nieukerken et al. 2006a) were usually identified as *S. betulicola*, most likely including misidentified leafmines of other species. No mines of *S. naturnella* were recorded from France before 2017.

It is certain that *S. naturnella* when discovered in the late 1930s, occurred in the alpine region of Italy and Austria and further north in Württemberg, an old record, often doubted, but proven to be correct here. The 1960 record in Moravia (Czechia) suggests that this record may belong to the original distribution area, which would include most of Austria and probably Hungary. In European Russia records occur since the 1990s, but before that almost nobody in Russia studied these small insects or their leafmines, so *S. naturnella* may well have been present earlier. Indeed the minimal variation in the DNA barcoding data throughout its range, with most variation being present in Russia, particularly the Far East, suggests that *S. naturnella* has spread from Siberia westwards relatively recently after the glaciations. When the current spread actually started is difficult to say, but the few records suggest that this was after 2000, from the alpine region Northwest into France and later Belgium and the Netherlands, and northward into Czechia, Poland and Germany. So far these expanding populations seem to show little or no variation in their DNA barcodes.

A fact that almost certainly contributed to overlooking the expansion of *S. naturnella* is the relatively difficult recognition of its leafmines, although Klimesch (1936, 1948) did describe them in detail, mentioning the important diagnostic features. Skala started to identify many leafmines as *S. naturnella*, but apparently made many mistakes (see above), contributing to the uncertainty of the identification of this species. The keys of Hering (1957) were of limited value, as important characters of egg position and frequent green coloration of the early mine were omitted. Another complication is the previously overlooked occurrence of *S. glutinosae* on *Betula*, a species often found together with *S. naturnella*, and with mines that are sometimes very similar. Identification of leafmines without larvae remains difficult at times, especially as it is based purely on the effect of the larva on the plant, which itself may be influenced by several external factors and the health of the larva. Caution, therefore, should be taken in using vacated leafmines for identification (especially for completely new records), i.e., without the benefits of larvae, reared adults or DNA barcodes. Plainly, studying a sample of leafmines in a population is always better than relying on a single specimen.

Fortunately, several old mine collections have been kept in good condition, notably the herbariums of Hering, Buhr and Wörz, so that it was possible to check old data and look for further records. That such collections exist is unfortunately not well known, collection managers are encouraged to register these collections online, with scans of the herbarium sheets (as e.g. done by Lödl and Gaal-Haszler (2010). Hopefully a study of more collections like these will provide better data about the spread of *S. naturnella*.

Our current knowledge of the distribution and spread of *S. naturnella*, owes much to the many naturalists who post photographs on the observation platforms, even when the identity of the species is unknown or uncertain. Observation platforms that are open to all taxa seem to be more effective than those to a single taxon, as it invites naturalists of all persuasions to contribute records of species they may otherwise have ignored. Moreover, many naturalists have either shifted their interest, e.g. from birds to moths, or simply enlarged their scope. The presence of active groups studying leafmines in the Netherlands and Belgium probably explains the difference compared with Germany for example, where few observations of this species were posted, and most records were cited in more traditional journal articles, books or on dedicated websites.

Factors to explain the expansion

Hibernation of adult *S. naturnella* has been observed from finding moths hidden under bark in the winter months in Belgium and The Netherlands and in early spring in Russia. Another indication is the fact that adults emerge in autumn soon after larvae have been collected (also noted by Klimesch 1936). Furthermore, the flimsy nature of the cocoon seems unsuitable to protect a hibernating larva or pupa. *Stigmella naturnella* is one of the few species of Nepticulidae that hibernates as an adult, which may have been a factor explaining its northward expansion following climate change. The only other European species that hibernates as adult is *S. aceris* (Frey, 1857), which has also expanded its range considerably. In this species, however, the expansion may be affected by other factors such as the massive planting of its *Acer* hostplant (van Nieukerken et al. 2006b). Such planting is unlikely to be a cause of the spread of *S. naturnella*, as *Betula* is a common native tree, spontaneously growing from seeds in many places. It is possible that *S. naturnella* is better adapted to dry conditions, and that the longer period of its hostplant being in leaf may provide

possibilities for having several annual generations, with more offspring that can disperse when the conditions are favourable. It is interesting to observe that most hibernating adults were seen in cities on planted *Platanus* trees, although observation may partly be explained by sampling bias, as the bark of these trees, easily removed, is often studied in winter to search for hibernating insects, compared with the study of forest trees at this time of year. Nevertheless, these city locality records remain interesting, as they are often distant from *S. naturnella*'s typical habitat, and thus can only be explained by dispersal.

Effects of the expansion

The density of leafmines on *Betula* at first sight seems to be low, except in exceptional circumstances, which would suggest that interspecific competition is unlikely. Various studies in the past rejected the importance of interspecific competition between herbivorous insects, but more recently ever more studies have found that competition is an important factor influencing the performance and fitness of herbivorous insects (Kaplan and Denno 2007). In their study of the ecology of birch-feeding *Stigmella*, Boomsma et al. (1987) found an ecological segregation of the involved species, and suggested that this may be due to the limited availability of suitable leaves for oviposition and development. In this situation, the sudden appearance of a relatively abundant leafminer as *S. naturnella* might disturb the population build-up of other *Stigmella* species, or even other herbivores that use the leaves (miners, gallers, etc.). Whether this is the case can only be studied by detailed monitoring of selected populations.

Of some concern during my fieldwork in the Netherlands was that I seldomly found species with a more northerly distribution, namely *S. lapponica* and *S. confusella* which, from casual experience, seemed to be more common before 2000. Such a decline might possibly be due to the warming climate and dry spring and summer of these years. Competition seems less likely in this case, as these species are usually found more commonly in wetter places than *S. naturnella* and more often on downy birch (*B. pubescens*).

The future

Stigmella naturnella is already established in much of Northwest Europe and we may expect a further northerly spread. Even during my fieldwork between 2020 and 2022 its distribution seems to have shifted ca. 50 km northwards. Birch stands in northern parts of the Netherlands, Germany and Poland should be examined for the presence of leafmines and larvae of *S. naturnella*, and it may soon arrive in Denmark, Sweden and the Baltic States and even the UK. At the same time it is important to fill in the gaps of knowledge in other parts of its distribution area.

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Appendix 1

Material of other species examined. *B.* = *Betula*. All in RMNH, unless otherwise mentioned.

Stigmella alnetella

ITALY • 2 larvae (barcoded), 2 leafmines; Roma, Manziano, Monumente Naturale della Caldera; 42.09066°N, 12.09733°E; alt. 265 m; 17 Sep. 2005; E.J. van Nieukerken leg.; *B. pendula*; EventId: EvN no 2005115-3M; RMNH.INS.11943–11944, 41122.

Stigmella betulicola

FRANCE • 4 ♂ 3 ♀, cocoons, leafmines; Sarthe, Le Mans, Arche de la Nature, Bois de Changé; 47.9888°N, 0.25835°E; alt. 83 m; 07 Oct. 2017; E.J. van Nieukerken & S. Richter leg.; *B. pendula*; emerged 26–28 Mar. 2018; EventId: EvN no 2017150-1K; RMNH.INS.16657–16663. RMNH.INS.16931, 44082.

NETHERLANDS • 1 ♀, 1 larva, 9 leafmines; Noord-Brabant, Goirle, Gorp en Roovert - Noord; 51.50512°N, 5.08499°E; 30 Sep. 2020; E.J. van Nieukerken leg.; *B. pendula*; emerged 24 Mar. 2021; EventId: EvN no 2020083-2H/K/M; RMNH.INS.17321, 31467, 48392, 48394.

Stigmella confusella

FINLAND • 4 leafmines; Satakunta, 1 km S of Harjavalta; 61.30944°N, 22.11056°E; alt. 30 m; 14 Sep. 2009; M. Kozlov et al. leg.; *B. pendula*; EventId: HAR-1S1, 2, 4; RMNH.INS.47667.

NETHERLANDS • leafmines; Noord-Brabant, Goirle, 4 km SW, Klooster Nieuwkerk; 51.487°N, 5.0278°E; 12 Sep. 1982; E.J. van Nieukerken leg.; *B. pubescens*; EventId: VU no. 82417-H; ZMA.INS.MIG.20330. • 1 larva, leafmine; Zuid-Holland, Leidschendam, Duivenvoordse en Veenzijdse Polder, Achterbos; 52.11051°N, 4.40236°E; 11 Aug. 2013; E.J. van Nieukerken leg.; *B. pubescens*; EventId: EvN no 2013098-3M; RMNH.INS.29702.

NORWAY • leafmines; Sogn og Fjordane, Stryn, Kjenndalen, at foot of glacier; 61.74188°N, 7.03083°E; alt. 180 m; 28 Jul. 2000; E.J. van Nieukerken leg.; *Betula*; EventId: EvN no 2000115-1H/K.

RUSSIA • 1 larva (DNA barcoded), leafmines; Leningrad Oblast, St. Petersburg, Sosnovka forest; 60.02456°N, 30.34481°E; 01 Jul. 2016; M. Kozlov & V. Zverev leg.; *Betula*; EventId: U101; RMNH.INS.31461, 47988–47989.

Stigmella continuella

NETHERLANDS • 2 larvae, 2 leafmines; Gelderland, Wekerom, De Valouwe, Immenkampweg; 52.08977°N, 5.71459°E; 16 Sep. 2020; E.J. van Nieukerken leg.; *B. pendula*; EventId: EvN no 2020062-4K; RMNH.INS.48324. • 1 larva, 5 leafmines; Limburg, Afferden, Zevenboomsveld; 51.64172°N, 6.03046°E; 24 Sep. 2008; E.J. van Nieukerken & C. Doorenbos leg.; *B. pubescens*; EventId: EvN no 2008107-1H/K; RMNH.INS.12832, 42296–42298.

Stigmella glutinosae

FRANCE • 1 larva (DNA barcoded), several leafmines; Cher, Villeneuve-sur-Cher; 47.02664°N, 2.22037°E; alt. 117 m; 30 Jul. 2009; E.J. van Nieukerken leg.; *B. pendula*; EventId: EvN no 2009039-H/L/M; RMNH.INS.17941, RMNH.INS.42780–42781. • 4 ♂ 1 ♀, 1 larva (DNA barcoded), 5 leafmines; Sarthe, Le Mans, Arche de la Nature, Bois de Changé; 47.9888°N, 0.25835°E; alt. 83 m; 07 Oct. 2017; E.J. van Nieukerken & S. Richter leg.; *B. pendula*; emerged 30 Mar.–16 Apr. 2018; EventId: EvN no 2017150-3K; RMNH.INS.16666–16669, 16749, 16933, 31076, 44086, 44196.

GERMANY • 3 leafmines; Berlin, Berlin-Dahlem, Botanischer Garten; 17 Aug. 1936; H. Buhr leg.; *B. papyrifera* [1 sample identified as synonym *B. excelsa*]; Herbarium Haussknecht. [originally as *Nepticula naturella*, Buhr 1940: 229] [identification tentative].

HUNGARY • 9 mines; Pest, Budapest SW: Kamaraerdö; 47.43972°N, 18.98404°E; 19 Oct. 1983; van Nieukerken & Boomsma leg.; *B. pendula*; EventId: VU no. 83523; ZMA.INS.MIG.11573.

ITALY • 30 leafmines; Roma, Manziano, Monumente Naturale della Caldera; 42.09066°N, 12.09733°E; alt. 265 m; 17 Sep. 2005; E.J. van Nieukerken leg.; *B. pendula*; EventId: EvN no 2005115-1H; RMNH.INS.41123 [identification tentative].

NETHERLANDS • 1 leafmine; Overijssel, Weerribben, Ossenzijl, Venebosch; 52.80696°N, 5.93349°E; 27 Aug. 2011; E.J. van Nieukerken leg.; *B. pubescens*; EventId: EvN no 2011117-6H; RMNH.INS.41655 [identification tentative].

RUSSIA • 2 leafmines; Lipetsk Oblast, Krasnoe Distr., Leski; 52.8729°N, 38.97°E; 11 Sep. 2014; L.V. Bolshakov leg.; *B. pendula*; RMNH.INS.47937. • 1 larva (DNA barcoded), 1 leafmine; Lipetsk Oblast, Usman Distr., Usman; 51.983°N, 39.783°E; alt. 165 m; 28 Aug. 2017; V. Zverev leg.; *B. pendula*; RMNH.INS.31159, 46143. • 2 leafmines; Lipetsk Oblast, Zadonsk Distr., Butyrki; 52.5724°N, 38.9582°E; 09 Aug. 2014; L.V. Bolshakov leg.; *B. pendula*; RMNH.INS.45798. • 2 larvae (DNA barcoded); Saratov Oblast, Saratov city, botanic garden; 51.565814°N, 46.005748°E; 29 Aug. 2020; V. Anikin leg.; *B. pendula*; EventId: VVZ_230a, VVZ_230b; RMNH.INS.31642, 31643. • 1 leafmine; Tula Oblast, Belyov Distr., Staroselye; 53.965°N, 36.1505°E; 22 Jul. 2008; L.V. Bolshakov leg.; *B. pendula*; RMNH.INS.45870. • 1 leafmine; Tula Oblast, Kimovsk Distr., Chebyshi; 53.7266°N, 38.6498°E; 24 Sep. 2009; L.V. Bolshakov leg.; *B. pendula*; RMNH.INS.45900. • 2 larvae (DNA barcoded), 5 leafmines; Tula Oblast, Kimovsk Distr., Lupishki; 53.8966°N, 38.5335°E; 09 Aug. 2012; L.V. Bolshakov leg.; *B. pendula*; RMNH.INS.31321, 31322, 45686. • 1 leafmine; Tula Oblast, Kurkino Distr., Vodyanoe Pole; 53.6176°N, 38.5766°E; 13 Aug. 2008; L.V. Bolshakov leg.; *B. pendula*; RMNH.INS.45830. • 1 ♂ (DNA barcoded), 3 leafmines; Ulyanovsk Oblast, Ul'yanovsk: "Vinnovka" City Park; 54.27°N, 48.03°E; emerged Jul. 2006; A. Mistchenko leg.; *B. pendula*; Genitalia slide: EvN4066; RMNH.INS.24066; Zolotuhin, V., personal collection. • 3 larvae (1 DNA barcoded), 38 leafmines; Voronezh Oblast, Voronezh; 51.583°N, 39.167°E; alt. 150 m; 28 Aug. 2017; V. Zverev leg.; *B. pendula*; RMNH.INS.31158, 44342, 44344.

Stigmella lapponica

PORTUGAL • 4 leafmines; Minho, Parc Nat. de Gerez; 07 Jul. 1980; J.W. Schoorl leg.; *B. pubescens*; EventId: VU no. 80180a; ZMA.INS.MIG.11586.

Photographed leafmines (not in collection): UNITED KINGDOM • occupied mine; England, Copley, North Dean wood; 7 Jun. 2018; Charlie Streets leg.; *B. pubescens*; <http://charlielepidopteraofcalderdale.blogspot.com/2011/11/neps-1.html>. – NETHERLANDS • occupied leafmine; Noordhollands Duinreservaat, Zuiderachterveld; 52.6557°N, 4.6343°E; 15 Jun. 2018; Wouter Bol leg.; *Betula* spec.; <https://waarneming.nl/observation/158901416/>.

Stigmella luteella

GERMANY • 1 leafmine; Hamburg, Botanischer Garten Hamburg; 28 Sep. 1932; H. Buhr leg.; *Betula utilis*; Herbarium Haussknecht. [originally as *Nepticula naturella*, Buhr 1940: 229]

NETHERLANDS • 1 ♂; 6 leafmines; Gelderland, Ede, Planken Wambuis, Mosselse Pad; 52.07214°N, 5.7576°E; 16 Sep. 2020; E.J. van Nieukerken leg.; *B. pendula*; emerged 30 Mar. 2021; EventId: EvN no 2020058-1H/K; RMNH.INS.17314, 48306, 48307. • 1 larva, 4 leafmines; Gelderland, Wekerom, De Valouwe, Immenkampweg; 52.08977°N, 5.71459°E; 16 Sep. 2020; E.J. van Nieukerken leg.; *B. pendula*; EventId: EvN no 2020062-2H; RMNH.INS.31451, 48320, 48321.

RUSSIA • 2 larvae (DNA barcoded), 6 leafmines; Karelia Rep., 20 km NW Nadvoitsy; 64.02893°N, 34.06971°E; 26 Aug. 2012; M. Kozlov et al. leg.; *B. pubescens*; EventId: R-64N-PUB-1; RMNH.INS.29972, 29973, 47901.

Stigmella sakhalinella

FINLAND [new record] • 1 leafmine; Helsinki, Linnanmäki park; 60.19108°N, 24.93797°E; 02 Sep. 2020; M. Kozlov & V. Zverev leg.; *Betula*; EventId: U06; RMNH.INS.47975. • 1 larva, 2 leafmines; Helsinki, Veikkola; 60.36153°N, 24.32469°E; 30 Jul. 2016; M. Kozlov & V. Zverev leg.; *Betula*; EventId: U01; RMNH.INS.47965. • 2 larvae, leafmines; Helsinki, 7 km SE Vihti, Ojakkala; 60.405°N, 24.3722°E; alt. 80 m; 01 Sep. 2017; M. Kozlov & V. Zverev leg.; *B. pendula*;

EventId: HCt; slide: 0; RMNH.INS.31157, 44352. • 8 leafmines; Salo, Hannilampi; 60.433°N, 23.433°E; alt. 94 m; 01 Sep. 2017; M. Kozlov & V. Zverev leg.; *B. pubescens*; EventId: Hki-Thu; RMNH.INS.44348.

NETHERLANDS • 12 leafmines; Utrecht, Soest, Korte Duinen S. edge; 52.15112°N, 5.32402°E; 23 Aug. 2021; E.J. van Nieukerken leg.; *B. pendula*; EventId: EvN no 2021122-2H/K; RMNH.INS.48701, 48702. • 1 larva, 4 leafmines; Zuid-Holland, Wassenaar, Hertenkamp; 52.14041°N, 4.38434°E; 10 Oct. 2018; E.J. van Nieukerken leg.; *B. pubescens*; EventId: EvN no 2018263-1H; RMNH.INS. 31282, 46553, 46554. • 2 larvae, 2 leafmines; Zuid-Holland, Wassenaar, Meijendel; 52.1374°N, 4.32566°E; 11 Oct. 2007; E.J. van Nieukerken leg.; *B. pubescens*; EventId: EvN no 2007122-1M; RMNH.INS.12647, 12648, 41480.

Supplementary material 1

DNA barcoded specimens of *Stigmella*

Authors: Erik J. van Nieukerken

Data type: table (excel file)

Explanation note: Dataset DS-STIGNATU on BOLDSYSTEMS (<https://doi.org/10.5883/DS-STIGNATU>), with details on Sample id's, Process id's, and Genbank Acession numbers of *Stigmella naturella* and some other relevant *Stigmella* specimens, cited in this paper.

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Link: <https://doi.org/10.3897/nl.46.99360.suppl1>

Supplementary material 2

Measurements and counts *Stigmella naturella*

Authors: Erik J. van Nieukerken

Data type: table (excel file)

Explanation note: Measurements of moths and leafmines of *Stigmella naturella*, and relevant other species; counts of egg positions on leaves.

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Link: <https://doi.org/10.3897/nl.46.99360.suppl2>

Supplementary material 3

Synecology of *Stigmella naturella*

Authors: Erik J. van Nieukerken

Data type: table (excel file)

Explanation note: Records of accompanying leafminer species on *Betula*, on sites where *Stigmella naturella* was found.

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